PHYLOGENETIC SYSTEMATICS OF *SCRAPTER* (HYMENOPTERA: ANTHOPHILA: COLLETIDAE)

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ABSTRACT

Scrapter Lepeletier de Saint-Fargeau & Audinet-Serville, 1828 (Hymenoptera: Aculeatea: Anthophila: Colletidae) is a genus of solitary bees largely endemic to southern Africa. This dissertation investigated the phylogenetic systematics of the genus. Eleven new species of *Scrapter* are described, principally from the Succulent Karoo biome of South Africa, bringing the total number of species in the genus to 42. An updated dichotomous key to facilitate identification is provided. The previously unknown females of *S. albifumus* Eardley and *S. amplispinatus* Eardley are also described. The genus is recorded from outside southern Africa for the first time with the collection of *S. nitidus* (Friese) in Kenya. This constitutes a significant range extension of the genus. The taxonomic status of five species described by Cockerell in 1944, and subsequently overlooked, is addressed. They are all found to be synonyms of other *Scrapter* species, except one, which is found to be a *Ctenoplectrina* species (Apidae: Apinae: Ctenoplectrini). The new synonymies are: *S. subincertus* Cockerell = *S. niger* Lepeletier de Saint-Fargeau & Audinet-Serville; *S. brunneipennis* Cockerell = *S. niger* Lepeletier de Saint-Fargeau & Audinet-Serville; *S. merescens* Cockerell = *S. leonis* Cockerell; *S. sinophilus* Cockerell = *S. algoensis* (Friese). *Scrapter ugandica* Cockerell becomes *Ctenoplectrina ugandica* (Cockerell) as a new combination.

Investigation of selected morphological features (e.g. postmentum, facial fovea, galea) revealed much diversity in *Scrapter*. The monophyly of *Scrapter* is not supported by unambiguous apomorphies, but is defensible by the congruence of various qualitative characters (e.g. premental fovea, T2 fovea, hindleg and sternal scopa in ♀, two submarginal cells).

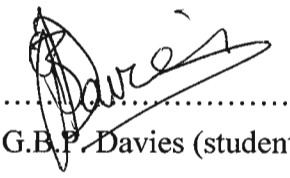
A cladistic analysis using 25 morphological characters recovered numerous most parsimonious trees under both equal- and successive-weighting. To aid in resolution, several taxa known from only one sex or from very limited material, and with many unknown states, were deleted from the matrix. Analysis using this reduced matrix under equal- and successive-weighting resulted in better resolution, although with low consistency index values. Several subclades were common to both cladograms, and likely represent monophyla. The low consistency indices and general lack of unique synapomorphies upholding these subclades, however, dictated against making any classificatory re-arrangements.

PREFACE

This dissertation represents the original work of the author. Where use has been made of the work of others it has been duly acknowledged in the text.

Research for this dissertation was conducted in the School of Biological and Conservation Sciences, under the supervision of Professor Denis Brothers. This dissertation has not been submitted, in part or whole, to any other University.

In accordance with Articles 8.2 and 8.3 of the *International Code for Zoological Nomenclature* (ICZN 1999), the nomenclatural acts proposed is this dissertation are disclaimed for the purposes of zoological nomenclature.



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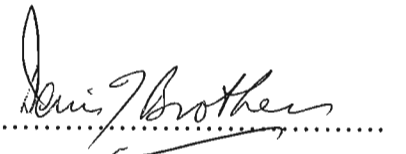

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LIST OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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CHAPTER 1

INTRODUCTION

Scrapter Lepeletier de Saint-Fargeau & Audinet-Serville, 1828 is a sizeable genus of small to medium-sized (3.5-14 mm long), non-metallic, ground-nesting, solitary bees (e.g. Fig. 1) that are largely endemic to southern Africa. The genus is part of the colletid monophylum, a grouping that has been given varying taxonomic rank, but traditionally at the family level as the Colletidae Latreille (e.g. Michener 2000; Engel 2001, 2005).

This dissertation provides an examination of the phylogenetic systematics of *Scrapter*, addressing the basic taxonomy and phylogenetic relationships of these bees. These objectives are achieved in the following sequence:

The current chapter first reviews the biology of *Scrapter*, then examines the relationships of the various colletid clades to place *Scrapter* in a broader phylogenetic context. The chapter concludes with the taxonomic history of the genus since its description in 1828.

In Chapter 2 materials and methodology are explained. Chapter 3 is a taxonomic chapter covering the description of new species, description of previously unknown females and the discussion of the status of five taxa described by Cockerell (1944*a*,*b*). Furthermore, an updated dichotomous key to the genus is presented and the discovery of *Scrapter* in East Africa announced.

Chapter 4 explores poorly known aspects of the morphology of *Scrapter*. Characters that are likely to be useful for resolving phylogenetic problems in the Colletidae (and broader Anthophila) are also discussed.

Chapter 5 presents an exploratory cladistic analysis of *Scrapter* based on 25 morphological characters that assesses suggested subdivisions of the genus proposed by various authors.

Most of this dissertation has already appeared in two papers (Davies *et al.* 2005; Davies & Brothers in press).

1.1. Biology of *Scrapter*

The life history of most *Scrapter* species is unknown. In the field, they are swift-flying bees that generally visit shallow, low-growing flowers and shrublets (pers obs). The only

published account of the nesting biology is that of Rozen & Michener (1968). These authors described the nests of three *Scrapter* species: *S. niger* Lepeletier de Saint-Fargeau & Audinet-Serville (= *S. longulus* Friese), *S. erubescens* (Friese) (= *S. crassulus* Cockerell) and *S. striatus* (= *S. alfkeni* (Friese)) found in late October and early November in the Western Cape, South Africa. The nest sites were in open, sandy areas with low shrubbery and the substrate was moist, 'so that excavated sand would hold its form, but water could not be squeezed out of it by hand' (Rozen & Michener 1968: 3). Nests of *S. niger* were the most common, the nests generally scattered, but some burrows were 'within a few inches' of each other. The main burrow of the nest was unlined, circular in cross-section and near-vertical. Lateral burrows radiated from the main tunnel at an angle and these laterals were filled with sand (lowermost left open). The brood-cell was merely a continuation of the lateral burrow and was lined with a single-layered, cellophane-like membrane. The pollen mass was dry on the inside but its surfaces, to a depth of about 0.25 mm, were moist. Cell construction and provision progressed downwards meaning that the oldest larvae were nearest the surface. The nests of *S. erubescens* were similar, but the provisions were reportedly 'a thick liquid throughout' (Rozen & Michener 1968: 8). Evidence of parasitism by the ammobatine genus *Sphecodopsis* Bischoff (Apidae: Nomadinae) was discovered. Generally-speaking, the nesting biology is similar to that of other ground-nesting colletids.

Scrapter has its greatest diversity in the winter rainfall Succulent Karoo biome (Rutherford & Westfall 1994; Milton *et al.* 1997) of the Western and Northern Cape, South Africa (Fig. 2). The Succulent Karoo is an arid region (annual rainfall ranging from 20-290 mm), with an exceedingly rich and highly endemic flora (Cowling & Hilton-Taylor 1994; Milton *et al.* 1997; Van Wyk & Smith 2001), and approximately 40% of the described *Scrapter* species are endemic to it. The biome is also rich in other indigenous bees and anthophilous insects, such as the distinctive megachilid tribe Fideliini (Whitehead & Eardley 2003; Engel 2004), masarine wasps (e.g. Gess 1992), and bombyliid and vermileonid flies (e.g. Stuckenberg 2000; Greathead & Evenhuis 2001).

Flower-visiting data of *Scrapter* are summarised in Table 1 (drawn from personal observations, specimen-label data, Eardley (1996) and Gess & Gess (2003)). For 12 species (29% of the genus) there are no floral data. Figure 3 shows a *S. chloris* Eardley female collecting pollen on *Grielum humifusum* Thunb. (Neuradaceae); this is a common sight in north-western South Africa (pers. obs).

Several noteworthy features emerge from Table 1. Asteraceae is by far the most frequented family with 11 *Scrapter* species recorded feeding on various composite genera. Within the composite-visiting taxa, there is no marked specificity (oligolecty), rather a

wide range of genera is visited (see, for example, inventory for *S. nitidus* (Friese)). Most of the composite genera have generalised, yellow, shallow, 'daisy-like' flowers.

The Zygophyllaceae are visited by three *Scrapter* species that are largely endemic to the Richtersveld. Proteas (Proteaceae) are little visited by bees in southern Africa (Gess & Gess 2003: 254-256), but two *Scrapter* species (*S. erubescens* (Friese) and *S. fuliginatus* Eardley) forage exclusively on *Leucadendron* and *Paranomus* spp. These two species appear to be sister-taxa, and together with *S. amplispinatus* Eardley, form a clade (see Chapter 5). *Scrapter amplispinatus* is evidently oligolectic to scrophularids in the genera *Polycarena* and *Selago*.

The type species for the genus, *S. bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, has been caught in large numbers exclusively on *Herrea* species (Aizoceae). This is reasonable indication that the species is oligolectic to *Herrea*. Although several other *Scrapter* species have been caught on Aizoaceae (Table 1), these are rare occurences. The Aizoceae have radiated extensively in western South Africa, and it is striking that so few *Scrapter* species visit these flowers.

Grielum (Neuradaceae) is frequented by a clade of three species (*S. chloris* Eardley, *S. luridus* Eardley, *S. whiteheadi* Eardley; see also Chapter 5). These bees are oligolectic on *Grielum* spp. Aside from these three species, only *S. avius* Eardley has been found on *Grielum*.

Examining the records of collected specimens (e.g. Eardley 1996) it is evident that those *Scrapter* species occuring in eastern South Africa have a flight period spanning the austral summer (November to March) corresponding to the main rainfall period in the east, whereas taxa in western South Africa fly during the austral winter and spring (July-October), corresponding to the main rainfall period in that part of the country. An exception are three species (*S. nitidus* (Friese), *S. ruficornis* (Cockerell) and *S. opacus* (Friese)), which have a long flight period (March to December).

1.2. Review of colletid relationships and classification

The colletid bees have traditionally been considered the clade of bees showing the most plesiomorphies, i.e. the sister-group to all the other bees (Michener 1944, 1965, 1979; Malyshev 1968; Engel 2001). In part, this view was based on the general similarity of glossae in colletids and sphecoid wasps, although McGinley (1980) indicated that the resemblance was possibly convergent.

Doubt has often been expressed that colletids are the sister-group to all other bees (e.g. Michener 2000: 85-86). The results from three nuclear genes presented by Danforth *et al.* (2006) have re-inforced this doubt. They showed that the sister-group to the other bees is probably the dasypodaine melittids (Danforth *et al.* 2006: fig. 3). These authors also found that the Melittidae was a non-monophylum, a conclusion reached independently by Alexander & Michener (1995). The supposition that melittids (or part of that group) are the sister-group to the other bees has been proposed before (e.g. Michener 1981*b*: 1). Several features of dasypodaine melittids such as the derived postmentum (excluding the intriguing *Samba* Friese), presence of an eversible endophallus and apparent lack of cocoon-spinning taxa are incongruous characters for the sister taxon to all other bees, but the molecular results appear robust. Unlike most ground-nesting bees, dasypodaine melittids notably do not line their brood cells with any lining; this is perhaps a plesiomorphic trait.

The colletids occupied a derived position in Danforth *et al's* (2006) cladograms; a similar result was also achieved in the consensus cladogram of Brothers (1999: fig. 8). Colletid monophyly is supported by the short, weakly bilobed, bifid or subtruncate glossa and unique features of the glossa such as the glossal lobes and brush (McGinley 1980). Further, the correlated habit of applying a largely clear, colourless, cellophane-like membane to their brood cells (e.g. Batra 1980; Torchio 1984; Torchio *et al.* 1988) is unique to colletids. The broad resemblance of the colletid glossa to that of apoid wasps that was once considered a symplesiomorphic resemblance must now be intrepted as a convergent feature on the basis of Danforth *et al's* (2006) molecularly-derived cladograms. Brady & Danforth (2004) have also reported the presence a spliceosomal intron in the F1 copy of the elongation factor-1 (EF-1) gene in all colletids sampled, but not in stenotritines or any other bee taxa (the diphaglossines were not sampled for this intron), a discovery that further strengthens belief in the monophyly of the colletids.

Aside from confidence in their monophyly, ideas on the internal phylogeny of the colletids have improved in recent decades, although the rank-based classification of the group remains unsatisfactory and contentious. Part of the problem confronting melittologists is that colletids are a phenotypically diverse group. Contrast, for example, the glabrous, 'wasp-like' euryglossines (Fig. 4) and hylaeines (Fig. 5) against the hirsute, quintessentially 'bee-like' *Colletes* (Fig. 6) and diphaglossines.

Following Michener (2000), five subfamilies are admitted (the most in any bee family); these being Colletinae, Hylaeinae, Euryglossinae, Diphaglossinae, and

Xeromelissinae. Michener (1944: 237, 2000: 161-163) placed *Scrapter* in the Colletinae amongst the 'paracolletine assemblage', a large group of mostly austral bees.

In an attempt to make the classification of bees more consistent with rank-based nomenclature in the wider Apoidea (Brothers 1999), Melo & Gonçalves (2005) only accepted a single, inclusive family of bees (and 25 subfamilies). Within their Colletinae, Melo and Gonçalves acknowledged seven tribes. They divorced the paracolletine bees from *Colletes* Latreille and *Mourecotelles* Michener (= Colletini) as the Paracolletini, and also gave *Scrapter* tribal status. Ascher & Engel (2006) have indicated that Melo and Gonçalves's scrapterine tribal designation failed the requirements of the *International Code of Zoological Nomenclature* (ICZN 1999), and their name is nomenclaturally unavailable.

Engel (2005), like Michener (2000), recognised several families of bees. Within his Colletidae, he admitted six subfamilies. Most notable was the erection of Scraptrinae Ascher & Engel to accommodate *Scrapter* (Ascher & Engel *in* Engel 2005: 13-14), and the inclusion of the stenotritine bees (Stenotritinae Cockerell) within a monophyletic Colletidae. The three competing classifications are summarised in Table 2.

What is the phylogenetic basis for these differing rank-based classifications? Before launching into a discussion of colletid phylogenies, a few words regarding each major colletid clade is required.

The euryglossines are rather elongate, mainly ground-nesting, wasp-like with reduced vestiture bees (Fig. 4) endemic to Australia (Michener 1965, 2000). The group is likely a monophylum as demonstrated by the presence of a distinctive, acuminate appendage on the dorsal edge of the basal part of the galea (Fig. 7), here named the *procurved galeal spine* (term suggested by M.S. Engel). This structure (of unknown function) represents a compelling apomorphy for the clade, and was briefly mentioned by Michener (2000: 210). Other notable morphological features include the blunt apex to the galeal blade (Fig. 7), the lack of a galeal velum in most genera, the pronounced, hairy lacinia (Fig. 7), lack of glossal lobes, the foveate prementum, the metabasitibial plate with edges delimited by a series of tubercles, strong galeal comb borne on an elevated crescentic sclerite, the slit-like facial foveae, two submarginal cells, the presence of a medio-longitudinal groove on tergum 1, lateral fovea on tergum 2 present in most (all?) genera and pygidial plate present in females.

The hylaeines are largely hairless, 'wasp-like' bees (Fig. 5) distributed throughout the world, that primarily nest in twigs, dry stems and other nooks. Support as a

monophylum is relatively weak, but the row of setae on the first two segments of the maxillary palp (McGinley 1981: 138; Alexander & Michener 1995: fig. 4) may be a useful apomorphy. These setae are, however, absent in some African *Hylaeus* species examined (pers. obs), and also apparently in some Australian taxa. The majority of hylaeine species lack metabasitibial and pygidial plates. The medio-longitudinal groove on tergum 1 is also absent. Most hylaeines lack vestiture on the face and have various patches of yellow maculation on the clypeus and paraocular areas. Like euryglossines, hylaeines have slit-like facial foveae, a foveate prementum, and a robust galeal comb on a crescentic sclerite.

The xeromelissines are tiny, slender, principally twig-nesting taxa (e.g. Eickwort 1967) restricted to the Neotropics. Ground-nesting taxa have only recently been described in this group (Michener & Rozen 1999; Packer 2004). Xeromelissines have a weak lacinia, poorly-developed galeal comb, foveate prementum, two submarginal cells, no medio-longitudinal groove on tergum 1 and no metabasitibial plate. The hindlegs are sparsely hairy, but these meagre setae do function as scopae. There is also a scopa on sterna 1-3.

The diphaglossines are large (except *Mydrosomella* Michener), hairy, Neotropical, ground-nesting bees. They are probably a monophylum on the basis of the deeply bifid glossa and tiny pterostigma (shorter than prestigma) (Michener 1986: 183) and various larval characters (McGinley 1981: 57). The nesting biology and larvae of the small, *Leioproctus*-like genus *Mydrosomella* may shed important phylogenetic light on the relationships of the diphaglossines (Michener 2000: 170).

The Colletinae (including paracolletines) are a large group of hairy, small to medium-sized, ground-nesting bees (Fig. 6) found throughout the world. Formerly, the group has been divided into two tribes (Colletini and Paracolletini). The Colletini, composed of *Colletes* and *Mourecotelles*, was characterised by its lack of metabasitibial and pygidial plates and prepygidial and pygidial fimbriae (in females). The paracolletines have 'no known synapomorphies' (Michener 1989: 625), and represent a group of hairy bees that are especially diversified in Australia and, to a lesser extent, in South America. Unlike *Colletes* and *Mourecotelles*, the metabasitibial and pygidial plates are usually present, sternum 7 in males often has two to four lateral lobes, a fairly well-developed galeal comb is present, there are strong scopae on the hindlegs, facial foveae are well-developed to absent, and the glossa is usually shallowly bilobed but occasionally deeply bifid. Michener (1965, 1989) and Maynard (e.g. 1991) have reviewed the taxonomy of Australian and South American paracolletines. The taxonomy of paracolletines remains

markedly unsatisfactory with many subgenera that grade into one another. The Colletinae has been the traditional domicile of *Scrapter* (Michener 1944, 2000).

The stenotritines are large, hirsute, ground-nesting bees endemic to Australia. Originally Michener (1944) included them as a colletid subfamily, but Houston (1975*a*), Houston & Thorp (1984), McGinley (1980), Torchio (1984) and Packer (2003) highlighted aspects of stenotritine biology and morphology that suggested these bees were best removed from the Colletidae. Noteworthy morphological features include the incompletely developed pre-episternal groove, lack of a glossal brush, pre-apical fringe and glossal lobes, divided basiglossal sclerite, long first flagellomere, reduced sting and the eversible endophallus of the male genitalia. Biologically, the most important difference is the absence of the cellophane-like lining of the brood cells, although 'a delicate transparent brownish membrane' can be separated with care from the cell walls (e.g. Houston & Thorp 1984: 377). The molecular evidence of Brady & Danforth (2004) and Danforth *et al.* (2006) also showed stenotritines do not belong in a monophyletic Colletidae.

Danforth *et al.* (2006: 365) stated that stenotritines are 'unambiguously sister to Colletidae', although the presence of two subantennal sutures that join above the clypeus ('a most remarkable feature', Michener 1944: 238), and the reduced sting (Packer 2003), is suggestive of the Andrenidae (the paracolletine *Leioproctus* (*Reedapis*) *semicyaneus* (Spinola) also has two apparent subantennal sutures forming a triangular subantennal area (Michener 1989: 657)). Whatever their correct position in the bee phylogeny, stenotritines have little to do with *Scrapter*. If accepted as the colletid sister-group, it does, however, potentially help in polarizing character states for resolving the colletid tree.

A variety of colletid phylogenies has been proposed. The intuitive phylogeny of Michener (1944: 230, diagram 13) is discussed first. Michener (1944: 228-229) believed colletids to be the most plesiomorphic bee lineage (now questioned by Danforth *et al.* 2006) and he listed 36 morphological features that he considered 'primitive' in bees. From this list Michener (1944) noted (p. 229) that the 'tribe Paracolletini possess practically all the [primitive] characters...the Paracolletini are consequently regarded as the most primitive group of bees...we need not necessarily postulate the characters of a hypothetical common ancestor of the colletids and other bees, so closely do some genera of this group approach the structure which we would suggest for such an ancestor'.

Despite this argumentation, Michener's phylogeny did not show the paracolletines as the sister-group to all the remaining colletids. Rather the phylogeny divided the colletids into two principal lineages consisting of (Xeromelissinae + (Euryglossinae + Hylaeinae))

and ((Stenotritinae + Diphaglossinae) + (Caupolicanini + (Colletini + Paracolletini))). Noteworthy features of this phylogeny included the combination of the large, fast-flying stenotritine and diphaglossine bees, and his placement of the Caupolicanini as the plesiomorphic sister-group of Colletini + Paracolletini. The Caupolicanini were soon moved to the Diphaglossinae (Michener 1954, 1966).

A broad-scale review of colletid phylogeny was not attempted again until McGinley's (1981) detailed revision of colletid larvae. McGinley presented several hand-derived cladograms. The Diphaglossinae were invariably the sister-group to all the colletids in his cladograms. A position as sister-group to all colletids is appealing as the diphaglossines are the only colletids to spin cocoons (Rozen 1984), a plesiomorphic trait widespread in apoid wasps. Diphaglossinae monophyly was strongly supported on larval grounds by the pronounced, spout-like salivary lips, presence of a salivary plate and the usually circular salivary opening (McGinley 1981: 57). The clade consisting of the Euryglossinae + Hylaeinae + Xeromelissinae was generally supported in most of his cladograms (e.g. McGinley 1981: figs 139, 140, 142, 144). The relationships of *Colletes* and the scrapterine, stenotritine and paracolletine bees were ambiguous, but the removal of *Scrapter* from the paracolletines was advocated given that *Scrapter* never grouped with those bees (e.g. McGinley 1981: figs 140-144). McGinley (1981: 160) intimated that *Scrapter* was possibly the sister-group to the Australian euryglossines based on the tuberculate metabasitibial plate found in some members of both these taxa. Furthermore, McGinley observed in *Scrapter* that there is a pronounced genal expansion posterior to the pleurostomal ridge, a characteristic 'unlike all other known bee larvae' (McGinley 1981: 83, fig. 51). This genal expansion is very likely an apomorphy for *Scrapter* (or a subset of the group), but the dearth of larvae makes it futile to pursue the matter. Overall, McGinley's conclusions were tentative, and he refrained from making formal changes to the colletid classification pending 'a cladistic reevaluation of adult characters' (McGinley 1981: xiii).

The principal modern phylogenetic analysis for 'short-tongued' bees is Alexander & Michener (1995). They examined 48 'short-tongued' bee genera, including 20 colletid genera (drawn from all subfamilies). They used two different analyses; Series 1 (109 morphological characters) adopted the 'Classical View' that the short, bilobed glossa was ancestral for bees. Series 2 (114 characters) adopted the 'Perkins-McGinley View' that such a glossa was derived. In brief, Perkins (1912: 97, 1919: 267-268) and McGinley (1980) had shown that males in several hylaeine genera (*Hemirhiza* Michener, *Meroglossa*

Smith and *Palaeorhiza* Perkins) have a short, acute glossa resembling andrenids, and they deduced that such an andrenoid glossa was the plesiomorphic condition in bees. Consequently, the broad, weakly bilobed to bifid glossa of most colletids was a convergent similarity to apoid wasps (specifically adapted to apply the transparent coating to the brood cells). As Michener (1992: 8) commented 'the male glossa has no known derived function differing from that of the female. It is the female's glossa that has apomorphic functions in nest construction, and therefore is likely to have apomorphic structures'. As discussed above, Danforth *et al.* (2006) have now provided strong molecular support for the Perkins-McGinley stance.

Unfortunately, Alexander & Michener (1995) reached few decisive conclusions concerning the Colletidae, and different parsimony tree-building procedures (e.g. equal- versus implied-weights) gave different cladograms. Further, Alexander and Michener (1995), regrettably, did not provide any indication of the synapomorphies supporting the various branches, leaving the reader ignorant of the characters upholding the clades. Not surprisingly, the general bee phylogeny differed strongly between Series 1 and 2 analyses (with Melittidae + 'long-tongued' bees representing the sister-group to all other bees in Series 2 analysis). Nevertheless, the colletid portions of the respective cladograms of Series 1 and 2 analyses using implied-weights were near-identical (Alexander & Michener 1995: fig. 6 vs fig. 15).

Under implied-weights in Series 2 (Alexander & Michener 1995: fig. 15), stenotritines were the sister-group to colletids. The colletids were recovered as a monophylum with two major colletid clades evident, consisting of Euryglossinae + (*Scrapter* + (Xeromelissinae + Hylaeinae))) and (Paracolletini + ((*Callomelitta* + Colletini) + (Diphaglossinae)). This is perhaps the best-supported morphological phylogeny for the Colletidae yet (Alexander & Michener 1995, fig. 15). The topology is shown in Figure 8. There are some notable similarities to McGinley's (1981) cladograms, viz. the Colletinae emerged as a non-monophylum, the euryglossines-hylaeines-xeromelissines generally formed a clade, and *Scrapter* never grouped with any of the included paracolletine genera (although sampling of the paracolletines, especially the diverse *Leioproctus*, was minimal). Unlike McGinley (1981), the Diphaglossinae never appeared as the most plesiomorphic clade in any of Alexander & Michener's cladograms. The cladogram is also congruent in many respects to the results of Danforth *et al.* (2006).

Contrariwise, Engel (2001, fig. 122) presented an intuitive phylogeny of the bees based on the traditional belief of colletids as the sister-group to other bees. The colletid

section revealed an unresolved polytomy of Colletinae + Stenotritinae + Diphaglossinae + (Euryglossinae + (Hylaeinae + Xeromelissinae)). *Scrapter* was not specifically identified in the cladogram. Engel (2001: 158) emphasised the non-monophyletic status of the Colletinae, and stated that 'the clade consisting of the "wasp-like" subfamilies of Hylaeinae, Euryglossinae, and Xeromelissinae is likely not to be plesiomorphic for [Colletidae] nor from where groundplan traits of all bees should be sought'. Engel (2001: 158) believed the stenotritines to be part of a monophyletic Colletidae and possibly 'sister to a clade of Australian colletines (e.g., some Paracolletini)', perhaps deriving this viewpoint from the larval analyses of McGinley (1981).

In their overview of insect evolution, Grimaldi & Engel (2005: fig. 11.82) presented another bee phylogeny, similar to Engel (2001), but with the modification that the Colletinae is sister to Stenotritinae + Paracolletinae. This diagram suggested most of the colletid cladogenesis took place during the Santonian-Campanian epochs (approximately 83-86 Mya), although a younger radiation may be more plausible using Danforth *et al's* (2006) findings. *Scrapter* is not reflected on this phylogeny.

From these disparate colletid phylogenies I draw the following tentative conclusions: (a) the colletids are diphyletic, one clade consisting of the xeromelissines, euryglossines and hylaeines, and another clade consisting of *Colletes*, *Mourecolletes*, paracolletines and diphaglossines; (b) the Colletinae as traditionally composed (e.g. Michener 2000) is not a monophylum; (c) the stenotritines are not true colletids, and, most relevant to this study, (d) *Scrapter* is related in some way to the euryglossine-hylaeine-xeromelissine clade (with the caveat that paracolletines have been poorly sampled in formal analyses to date).

1.3. Historical review of *Scrapter*

Scrapter has endured a long and rather turbulent nomenclatural and taxonomic career, as partly documented by Cockerell (1932*a*), Eardley (1996) and Michener (1997). Confusion was rife in the late 1800s and early 1900s as what type of bee the name *Scrapter* pertained to.

Amédée Lepeletier de Saint-Fargeau and J.G. Audinet-Serville (1828: 403-404) described the genus *Scrapter*, and introduced three species (*S. bicolor*, *S. punctatus* and *S. niger*), and also observed that *Andrena lagopus* Latreille belonged in the genus. Two of the species (*S. bicolor* and *S. niger*) were from Africa, while *S. punctatus* and *S. lagopus* were European taxa. Lepeletier de Saint-Fargeau and Audinet-Serville correctly inferred that

Scrapter was probably a ground-nesting taxon, the name *Scrapter* being derived from the Greek *skapter* meaning digger or burrower ('ce genre dont le nom vient d'on mot grec qui signifie: fouisseur'). Thirteen years later, in a regrettable move, Lepeletier de Saint-Fargeau (1841: 260) used the name *Scrapter* again for a new genus based on *Scrapter brullei* Lepeletier, 1841 from the Canary Islands. This unfortunate action would precipitate much future uncertainity.

Smith (1853: 120-121) provided a short description of *Scrapter*, and recognised nine species in the genus in his catalogue of Hymenoptera in the British Museum, London (The Natural History Museum). He unfortunately combined under *Scrapter* the taxa described by Lepeletier de Saint-Fargeau & Audinet-Serville (1828), Lepeletier de Saint-Fargeau (1841) and two *Andrena* Fabricius species introduced by Lucas (1849: 179). This resulted, unsurprisingly, in an artificial assemblage. Smith's description of the labium was clearly of a non-colletid ('labium elongate-lanceolate'), and this is confirmed by reference to his illustration of the proboscis of '*Scrapter*', which shows a short, pointed andrenoid glossa (Smith 1853, plate 4, figs 16-17).

Vachal (1897) investigated the status of *Scrapter* and expressed surprise at Lepeletier de Saint-Fargeau's (1841) action, pointed out discrepancies between the two descriptions of *Scrapter* and incisively noted that *S. brullei* was really a *Panurginus* species (Andrenidae: Panurginae), as later confirmed (Michener 2000). Vachal (1897: 63) designated *S. bicolor* as the type species of *Scrapter*, but was evidently unable to examine the Lepeletier de Saint-Fargeau and Audinet-Serville type specimens.

In his landmark work, *Die Bienen Afrikas*, Friese (1909: 124) provided another early description of *Scrapter* when he described *Polyglossa* ('multiple tongues') as a new genus, which would later prove to be a synonym of *Scrapter*. Friese observed that *Polyglossa* reminded him more or less of an *Andrena* or *Halictus* Latreille species ('im Habitus erinnem alle Arten mehr oder weniger an *Andrena* und *Halictus*'), but the blunt, bilobed glossa ('stumpfe zweiteilige Zunge') indicated it was an 'urbiene' ('primitive' bee) related to *Colletes* Latreille.

Friese provided a good illustration of the proboscis of *Polyglossa*, lucidly showing the weakly-bilobed glossa and thick glossal brush (Friese 1909, fig. 1). He also illustrated (fig. 19) the galea of *Polyglossa capensis* Friese showing a strong galeal comb of approximately 15 teeth (this observation would later be overlooked by other authors). Otherwise, Friese's description concentrated on wing-cell structure and basic composition of the mouthparts, but it is too superficial for effective comparison against other colletids.

The name *Scrapter* does appear in Friese's work, but he based his conception of the genus on Lepeletier (1841). Friese (1909: 184-190) synonymised *Ctenoplectra* Kirby (now Apidae) with *Scrapter* Lepeletier (1841), and placed *Scrapter* between *Samba* Friese (now Melittidae) and *Ceratina* Latreille (now Apidae). Friese nevertheless retained *S. bicolor*, *S. niger* and *S. striatus* Smith with the non-colletid bees, and merely quoted the original descriptions verbatim, even though two of these (*S. bicolor* and *S. niger*) had been described in 1828 before *Scrapter* Latreille 1841.

Friese (1912) erected *Strandiella* as a genus distinct from *Polyglossa*, but provided little justification for this action. The type species was designated as *Strandiella longulus* Friese (= *Scrapter niger*) by Cockerell (1916: 430). Cockerell (1921: 203), like Friese, underlined that *Polyglossa* was a colletid with similarity to *Andrena* in body form: '*Polyglossa* consists of bees having the appearance of *Andrena*, but with only 2 submarginal cells, and the tongue formed as in *Colletes*'. Cockerell (1921) made *P. capensis* Friese the type species of *Polyglossa*.

Friese (1925: 513) synonymised *Strandiella* with *Polyglossa*, but retained *Strandiella* as a subgenus ('die beiden Gattungen *Polyglossa* und *Strandiella* sehr engmiteinander verbunden sind, ja am besten wohl zu einer Gattung *Polyglossa* vereinigt werden'). Friese (1925: 514) recognised 21 species of *Polyglossa*, with 15 of them contained in the subgenus *Strandiella*. In his key to the species of *Polyglossa*, Friese (1925: 514) separated *Strandiella* from *Polyglossa* on the feeble basis of its narrower, *Halictus*-like body, reduced hairiness on the femur and the 'flocculus' almost absent.

Brauns (1929: 134) collected specimens of *Polyglossa heterodoxa* Cockerell in the Somerset West district, Western Cape. Brauns thought the female was similar to other *Polyglossa* species, but he contended that the male showed substantial differences (especially in its armature on the hindlegs), and therefore created a new subgenus *Parapolyglossa* ('wurde es mir klar, daß diese Biene, obwohl sie im ♀ Geschlechte völlig mit *Polyglossa* übereinstimmt, das ♂ der zahllosen Arten des Genus abweicht, daß ich das folgende subgenus darauf errichte'). Within *Parapolyglossa*, Brauns united those species with armed legs in the males known to him, viz. *S. heterodoxus* and *S. armatipes* (Friese) (= *Polyglossa namaqua* Brauns). As pointed out by Eardley (1996: 39), Brauns curiously characterised the species (on p. 132) as *Parapolyglossa heterodoxa* as if *Parapolyglossa* was a full genus.

Cockerell (1930*a*; also 1932*b*: 453) again likened *Strandiella-Polyglossa* to *Andrena* in body form: 'without examining the mouthparts, any one might take a

Strandiella for an Andrenid with two cubital cells'. At about the same time, Cockerell (1930b: 49) referred back to Lepeletier de Saint-Fargeau and Audinet-Serville's original description and astutely deduced 'on reading [their] description...that *Scrapter* was really the genus *Strandiella* of Friese, although it included a mixture of things'.

Monsieur Benoist 'hunted up' the types in the Paris Museum on Cockerell's behalf and located the original specimens (although they lacked type labels). Benoist indicated that *Scrapter bicolor* had an obtuse tongue, and therefore was evidently a colletid, the proboscis of *S. niger* could not be seen, and *S. perpunctatus* had a pointed glossa and was unequivocally an *Allodape* Lepeletier de Saint-Fargeau & Audinet-Serville in Benoist's opinion. Cockerell considered the enigma of *Scrapter* virtually resolved, and later he was able to examine the original specimens in Paris himself (Cockerell 1932*a*). Cockerell's examination fully endorsed Benoist's diagnosis, and he formally synonymised *Strandiella* with *Scrapter*. Strangely, Cockerell had evidently ignored Friese's (1925) sinking of *Strandiella* to subgenus level within *Polyglossa*.

Till this stage the phylogenetic relationships of *Scrapter* within the colletids had not been addressed. In this respect, Cockerell & Ireland's (1933) paper was an important first step in resolving the relationships of *Scrapter*. Cockerell & Ireland (1933: 973) observed 'that the African genus *Scrapter*, Lepeletier and Serville, showed much resemblance to the Australian *Euryglossidia* Cockerell. In fact, on superficial examination they were not easy to separate' (despite the genus name, *Euryglossidia* is a paracolletine and not an euryglossine; Michener 2000). Cockerell & Ireland, however, argued against any close relationship because of differences in labrum shape, the more curved mandibles with a broader pre-apical tooth in *Euryglossidia*, the bigger galeal comb, long maxillary palpi of *Euryglossidia* and minute differences in wing venation (some of these putative differences are, in point of fact, not valid). *Euryglossidia* are small, weakly metallic bees with pectinate inner metatibial spurs and lacking facial foveae (Michener 1965: 68), features that are not at all suggestive of *Scrapter*.

Cockerell (1934: 452), in yet another of his 'abominable...little notes' (Wheeler *in* Evans & Evans 1970: 143), made *Polyglossa* a subgenus of *Scrapter* in describing *S. leonis* Cockerell, although he did not elaborate on this decision.

In his watershed reorganisation of the Anthophila, Michener (1944: 237) placed *Scrapter* in the Colletinae, but understandably did not say more on the matter in this broad-ranging paper. In a comprehensive review of the Australian bee fauna, Michener (1965: 39) remarked that the large paracolletine genus *Leioproctus* Smith 'probably also includes

some species, currently placed in *Polyglossa*, from South Africa'. After this point, taxonomic studies on *Scrapter* entered a two-decade-long nadir.

Interest in *Scrapter* was revived by Eardley's detailed taxonomic revision of the genus (Eardley 1996). Numerous important advances were made in this paper including the formal synonymisation of *Polyglossa* with *Scrapter*, provision of a 'generic diagnosis', description of 11 new species and the synonymisation of 23 species names. The distribution of species were plotted and the terminalia of the genus illustrated for the first time.

Michener (2000: 161-163) retained *Scrapter* in Colletinae and provided a useful precis of the group. Michener (2000: 162) also suggested that 'in a general way *Scrapter* is divisible into two major groups' and provided characters he believed indicated this. This supposition is evaluated in Chapter 5.

Ascher & Engel (*in* Engel 2005) separated *Scrapter* as a monogeneric subfamily, Scraptrinae. They argued that the morphological diversity warranted dissolving the group into several subgenera (Engel 2005: 13), a view also expressed by Melo & Gonçalves (2005: 157), but Ascher and Engel did not pursue this idea.

The history and typification of the names applied to the group are summarised in Table 3.

CHAPTER 2

METHODOLOGY

Pinned adult specimens were used in the study. Specimens were examined using a Wild TYP 181300 dissecting microscope, with illumination provided by a Volpi Intralux 5000 light source. Line drawings were executed using a Wild drawing tube (*camera lucida*). Measurements were made with a calibrated eye-piece graticule. Morphological terminology follows standard melittological references e.g. Eickwort (1969: 338-374), Engel (2001: 19-33) and Michener (1944: 158-196, 2000: 40-52). Several terms, however, need some elucidation. The term *anterior face of supraclypeal area* refers to the anterior side of the raised supraclypeal area, which is a bulbous, generally convex protuberance (Fig. 9); it frequently has distinctive sculpture or patterning. In some *Scrapter* species, the supraclypeal area is flat and this term is not applicable. The term *carinulate*, in describing surface sculpture, refers to largely parallel, longitudinal ridges packed fairly close together.

In species descriptions, bilaterally symmetrical structures are described in the singular. Abbreviations used: T—tergum (e.g. T1, T2), S—sternum (e.g. S1, S2), F—flagellomere (e.g. F1, F2), sp.—species (singular), spp. —species (plural), sp. n.—species novum (new species). The term *terminalia* has been used broadly to include T7-8 and sting (in ♀♀) and S6-8 and genitalia (in ♂♂). Terminalia (of both sexes) were removed from relaxed specimens, immersed in cold 10% KOH for approximately 24 hours, neutralised with dilute acetic acid and rinsed in water. Terminalia were stored in microvials attached to the pin of the specimen. Measurements in the species descriptions largely follow the guidelines of Michener (2000: figs 10.3b, 10.8); head length is *sensu* Michener, i.e. top of vertex to ventral edge of clypeus and not a longitudinal measurement.

Specimens for SEM examination were sputter-coated with gold-palladium and examined using a Phillips XL 30 ESEM at a working voltage of 10-15kV. Details of cladistic procedure are explained in Chapter 5.

Material examined was obtained from the following collections: Albany Museum, Grahamstown, South Africa (AMGS); Denis Brothers Private Collection, University of KwaZulu-Natal, Pietermaritzburg, South Africa (DJBC); Michael Kuhlmann Private Collection, University of Muenster, Germany (MKPC); The Natural History Museum, London, United Kingdom (NHML); Natal Museum, Pietermaritzburg, South Africa (NMSA); South African Museum, Cape Town, South Africa (SAMC) and National Collection of Insects, Tshwane (formerly Pretoria), South Africa (SANC).

CHAPTER 3

ASPECTS OF THE TAXONOMY OF *SCRAPTER*

In this chapter, 11 new species of *Scrapter* are described. A revised dichotomous key for the identification of *Scrapter* species is provided. The previously unknown females of *S. albifumus* Eardley and *S. amplispinatus* Eardley are described. Five species described by Theodore Cockerell in 1944, and overlooked in Eardley's (1996) revision, are dealt with. Lastly, the discovery of *Scrapter* outside of southern Africa (i.e. north of the Zambezi-Cunene rivers), based on a single female specimen, is announced.

3.1. Description of *Scrapter*

Three useful descriptions or diagnoses of *Scrapter* now exist (Eardley 1996: 38-39; Michener 2000: 161-163; Ascher & Engel *in* Engel 2005: 13). All of these contain inaccuracies, and thus a comprehensive description is provided here. Fuller information on variable characters (noted as 'varied' in the description) is provided in Chapter 4.

Body length 3.5-14 mm. Integument usually black or blackish. Legs frequently with yellow tarsomeres and tibiae. Clypeus and paraocular areas never with any yellow maculation. Metasoma black, red or orange-red. Integument never with metallic irridescence. Sexual dimorphism slight to pronounced, ♀ or ♂ may be the larger sex. Flagellum of female 10-segmented and male 11-segmented. Labrum varied. Single subantennal suture directed toward medial, lower margin of antennal socket (Fig. 10). Anterior tentorial pit located high on epistomal sulcus (Fig. 10). Malar area (space) absent (i.e. base of mandible articulates very close to ventral margin of compound eye). Mandibular structure varied. Facial fovea present but shape varied. Lacinia present on dorsal margin of stipes, structure varied. Glossa short, subtruncate to weakly bilobed. Ventral (posterior) surface of prementum with fovea in both sexes. Galeal comb present, size not uniform. Postmentum a flat plate or a complex structure with lateral panels and posterior process. Maxillary palp six-segmented, varied in length, falling short of galea apex, or exceeding it. Labial palp four-segmented. Cardo with inner process moderately produced (Figs 11, 12). Pronotum varied. Propodeum strongly angulate to declivitous. Pre-episternal groove long extending to near the post-coxal process (Fig. 13). Female with brush on anterior (outer) side of probasitarsus, structure of setae varied. Metabasitibial plate present in all taxa but form varied. Female scopa from metatrochanter to metatibia, also on S2. Long, simple keirotrichia in female on metatibia. Arolia present. Pretarsal

claws deeply cleft in male, variable in female (simple to cleft). Posterior (inner) metatibial spur in female ciliate (Fig. 14). Male metafemur and metatibia simple or with processes (armature). Metabasitarsus scarcely wider than following tarsomeres (metamediotarsus 0.95X width of metabasitarsus). Two submarginal cells. Jugal lobe approximately 0.75-0.90X length of vannal lobe. Anterior surface of T1 broadly concave with medio-longitudinal groove. Prepygidial fimbria present in females. Pygidial plate present in females and some males. Fovea on sides of T2 (Fig. 15) present, absent in *S. tomentum* and *S. albifumus* and reduced in male *S. heterodoxus*. Gradulus on T2 far removed from spiracle but not directed backward at the side (Fig. 16). No or two apicolateral lobes on male S7.

3.2. Revised key to the species of *Scrapter* (adapted from Eardley 1996)

1a. Males (antennal flagellum 11-segmented; no metatibial scopa).....2

1b. Females (antennal flagellum 10-segmented; scopa present on metatibia) 41

2a. Metatibia tuberculate apically (Fig. A).....3

2b. Metatibia not modified (Fig. B).....7

3a. Mesobasitarsus greatly swollen, yellow (resembling grotesque yellow balloon) .....***S.armatipes*** (Friese)

3b. Mesobasitarsus unmodified 4

4a. All tibiae and tarsi yellow to yellowish-orange; small bee (body length approximately 5 mm).....***S.aureiferus*** Cockerell

4b. All tibiae and tarsi black; medium to large bee (body length approximately 7-14 mm).....5

5a. Metabasitarsus strongly swollen; vertex and frons carinulate ....***S. amplitarsus*** (Friese)

5b. Metabasitarsus not greatly swollen; vertex and frons not carinulate.....6

6a. Large (body length 9-14 mm), robust, very hirsute bee; strongly swollen metafemur.....***S. heterodoxus*** (Cockerell)

6b. Medium-sized (body length approximately 6.5 mm), elongate, moderately

hirsute bee; metafemur not swollen ..... ***S. acanthophorus*** sp. n.

7a. T2-T5 almost completely covered in dense pubescent tomentum (as opposed to longer setae); metasoma black ..... ***S. caesariatus*** Eardley
7b. T2-T5 either without tomentum (may be otherwise hairy), or each tergite with basal tomentum only; metasoma black or partially red 8

8a. S2 densely covered in fine, very thick vestiture throughout sternum, contrasting strongly with other sterna (found in savanna areas of northern South Africa and Zimbabwe) ..... ***S.absonus*** Eardley
8b. S2 bare to moderately hirsute (not strongly differentiated from other sterna) 9

9a. Propodeal triangle greatly modified with central area much reduced, triangle forming three acute points (Fig. C) 10
9b. Propodeal triangle not modified, forming a roughly equilateral triangle (Fig. D) 12

10a. Anterior (outer) metatibial spur strongly swollen (Fig. E); apical quarter of wing obfuscated ..... ***S. amplispinatus*** Eardley
10b. Anterior (outer) metatibial spur not strongly swollen (Fig. F); entire wing hyaline 11

11a. Metasoma partly red; propodeum dark black but lacking velvety black vestiture .. ***S. erubescens*** (Friese)
11b. Metasoma black; propodeum with velvety black vestiture ..... ***S. fuliginatus*** Eardley

12a. Clypeus greatly reduced (concave ventrally); scape black (Fig. G) ..... ***S. chloris*** Eardley
12b. Clypeus unmodified or, if somewhat reduced; scape yellow (Fig. H) 13

13a. Antennal scape yellow or orange anteriorly 14
13b. Antennal scape black 15

14a. Metasoma orange; body length approximately 6 mm; no lateral pronotal ridge.....
.....***S. pyretus*** sp. n.
14b. Metasoma black; body length approximately 8-9 mm; sharp and well-defined lateral pronotal ridge.....***S. luridus*** Eardley

15a Pronotal lobe yellow 16
15b. Pronotal lobe black or red-brown 18

16a. Mesoscutum generally densely punctate (punctures mostly less than a puncture diameter apart), very finely sculptured between punctures; metasoma orangish to black..
.....***S. flavipes*** (Friese)
16b. Mesoscutum sparsely punctate (punctures mostly more than puncture diameter apart); smooth between punctures, metasoma black 17

17a. Robust bee (body length approximately 8-9 mm); metafemur partly yellow and metatibia completely yellow.....***S. basutorum*** (Cockerell)
17b. Smallish bee (body length approximately 5-5.5 mm); metafemur black and metatibia partly black .....***S. flavostictus*** Cockerell

18a. Propodeum declivitous (vertical) (Fig. I).....19
18b. Propodeum weakly to strongly angulate (weakly angulate propodeum requires careful discrimination) (Fig. J) 21

19a. Clypeus not bearing ventrolateral protuberances; facial fovea distinct; S8 bifurcate anteriorly (Fig. K).....***S. capensis*** (Friese)
19b. Clypeus with ventrolateral projections; facial fovea weakly differentiated from surrounding integument; S8 rounded or pointed anteriorly (Fig. L) 20

20a. Metasoma black; mesosoma vestiture conspicuously orange-brown .....
.....***S. thoracicus*** (Friese)
20b. Metasoma mostly orange-red; mesosoma vestiture whitish.....
.....***S. bicolor*** Lepeletier and Serville

21a. Clypeus with mediolongitudinal sulcus present (sulcus may be weakly defined, careful scrutiny sometimes required) (Fig. M) 22

21b. Clypeus with mediolongitudinal sulcus absent (Fig. N) 25

22a. S7 concave posteriorly (Fig. O), lacking posterolateral projections ..... ***S. pallidipennis*** (Cockerell)

22b. S7 very weakly concave posteriorly with posterolateral projections (Fig. P) 23

23a. Mesoscutum fairly densely punctate (interspace <1X puncture diameter) ..... ***S. nitidus*** (Friese)

23b. Mesoscutum sparsely punctate (interspace >1X puncture diameter) 24

24a. Antenna short (slightly longer than eye); notaulus and median line strongly impressed ..... ***S. ruficornis*** (Cockerell)

24b. Antenna long (about twice as long as eye); notaulus and median line weakly impressed ..... ***S. opacus*** (Friese)

25a. Antenna ventrally yellow except for black apical part of F9 and all of F10-11 (creating characteristic colour pattern; Fig. Q) 26

25b. Antenna ventrally all or mainly yellow (Fig. R), or all dark orange-brown 28

26a. Antenna exceedingly long reaching T3; mandible largely yellow ..... ***S. chrysomastes*** sp. n.

26b. Antenna not extending beyond propodeum; mandible all blackish 27

27a. S7 deeply concave posteriorly; S8 pointed anteriorly; tiny bee (body length <6.5 mm); dead specimens usually curl on pin ..... ***S. albifumus*** Eardley

27b. S7 weakly concave posteriorly; S8 rounded anteriorly; medium-sized bee (body length >6.5 mm); dead specimens do not curl on pin ..... ***S. tomentum*** Eardley

28a. Vertex and frons distinctly carinulate 29

28b. Vertex and frons not carinulate 35

29a. S7 concave posteriorly 30

29b. S7 posteriorly with single or two small, acute projections 34

30a. Clypeus strongly protuberant 31
30b. Clypeus not to weakly protuberant 32

31a. Mesosomal setae largely orange-brown ..... ***S. carysomus*** sp. n.
31b. Mesosomal setae black ..... ***S. eremanthedon*** sp.n.

32a. Metabasitibial plate not entire (only posterior carina) (Fig. S); meso- and metatibia dark (all tarsi may be yellow); mesoscutum punctation dense ..... ***S. niger*** Lepeletier and Serville
32b. Metabasitibial plate entire (Fig. T); tibiae yellow or black (tarsi may be yellow); mesoscutum punctation sparse or dense 33

33a. Legs all black; mesoscutum punctation dense ..... ***S.viciniger*** sp. n.
33b. All tibiae and tarsi yellow; mesoscutum punctation sparse ..... ***S. glarea*** sp. n.

34a. S7 with single acute point posteriorly; facial fovea indistinct (poorly differentiated from surrounding integument) ..... ***S. oxyaspis*** sp. n.
34b. S7 with two tiny acute projections posteriorly; facial fovea shallow and broad (well differentiated from surrounding integument) ..... ***S. striatus*** Smith

35a. Body length >6.5 mm ..... ***S. algoensis*** (Friese)
35b. Body length <6.5 mm 36

36a.Mesoscutum integument finely reticulate ..... ***S. albitarsis*** (Friese)
36b. Mesoscutum integument smooth 37

37a. Propodeal triangle rough reticulate sculpture medially 38
37b. Propodeal triangle smooth and shiny medially 40

38a Metabasitibial plate entire ..... ***S. sittybon*** sp. n.
38b. Metabasitibial plate not entire (posterior carina only) 39

39a. Metasoma black; S7 truncate posteriorly, no posterolateral projections .....
.....***S. avius*** Eardley
39b. Metasoma partially red; S7 weakly concave posteriorly.....***S. pruinosus*** sp. n.

40a. Flagellomere 11 round apically (Fig. U).....***S. calx*** Eardley
40b. Flagellomere 11 elongate and tapering to acute point (Fig. V) .....
..... ***S. catoxys*** sp. n.

41a. Propodeal triangle strongly incurved laterally, forming three acute points
(Fig. C), or triangle difficult to distinguish from adjoining propodeum 42
41b. Propodeal triangle not modified (triangular), distinct from propodeum (Fig. D) ...45

42a. Mesoscutum smooth between punctures .....***S. amplitarsus*** (Friese)
42b. Mesoscutum reticulate or roughened between punctures.....43

43a. Clypeus dull; facial fovea indistinct and difficult to discern .....
.....***S. fuliginatus*** Eardley
43b. Clypeus shiny; facial fovea distinct and easily discernable.....44

44a. Metasoma all black, dull, roughened sculpture .....***S. amplispinatus*** Eardley
44b. Metasoma often partly reddish, shiny, finely roughened sculpture.....
.....***S. erubescens*** (Friese)

45a. Clypeus with mediolongitudinal sulcus (may be weakly developed) (Fig. M) .....
.....46
45b. Clypeus without mediolongitudinal sulcus (Fig. N).....54

46a. Distinct posterior hair-bands on marginal zones of terga .....
.....***S. heterodoxus*** (Cockerell)
46b. Terga without distinct posterior hair-bands (sparse bands may be present).....47

47a. Pronotal lobe yellow 48
47b. Pronotal lobe black or blackish 49

48a. Mesoscutum punctation sparse (interspace >2X puncture diameter); facial fovea broad and shallow ..... ***S. basutorum*** (Cockerell)
48b. Mesoscutum punctation very dense (interspace approximately 0.5-1X puncture diameter); facial fovea rather narrow ..... ***S. flavipes*** (Friese)

49a. Clypeus protuberant ..... ***S. caesariatus*** Eardley
49b. Clypeus not protuberant 50

50a. Clypeus with small tubercle medioventrally; metabasitibial plate consisting of small tubercles ..... ***S. niger*** Lepeletier & Serville
50b. Clypeus with medioventral margin unmodified; metabasitibial plate entire or comprised of distinct carinae 51

51a. Mesoscutal punctation usually fairly dense (interspace <1X puncture diameter); metasoma completely black or black and reddish; metatibial scopa usually white anteriorly and infuscated dorso-posteriorly ..... ***S. nitidus*** (Friese)
51b. Mesoscutal punctation sparse (interspace >1X puncture diameter); metasoma always black; metatibial scopa usually black or white (white scopa may be lightly infuscated posteriorly) 52

52a. Metatibial scopa black; vestiture on T5-T6 black ..... ***S. ruficornis*** (Cockerell)
52b. Metatibial scopa white; vestiture on T5-T6 white 53

53a. Medial region of propodeal triangle smooth ..... ***S. opacus*** (Friese)
53b. Medial region of propodeal triangle with transverse carinae .....
..... ***S. pallidipennis*** (Cockerell)

54a. Metasoma largely reddish 55
54b. Metasoma black or blackish 62

55a. Metatibial scopa all black; facial fovea broad and shallow .....
..... ***S. bicolor*** Lepeletier & Serville
55b. Metatibial scopa all white or white with dark ridge dorso-posteriorly; fovea narrow or narrowish 56

56a. Mesoscutum with roughened sculpture between punctures.....57
56b. Mesoscutum smooth between punctures (may be very finely reticulate, but not roughened).....58

57a. Metatibial scopa white; prepygidial fimbria white.....***S. luridus*** Eardley
57b. Metatibial scopa white anteriorly, infuscated dorso-posteriorly; prepygidial fimbria black.....***S. chloris*** Eardley

58a. Mesoscutum largely punctureless; metabasitibial plate entire and very hairy .....
.....***S. calx*** Eardley
58b. Mesoscutal punctation fairy dense to dense; metabasitibial plate delimited by tubercles or weak carinae.....59

59a. Body length approximately 8-8.5 mm; brownish vestiture on mesosoma dorsum.....
.....***S. whiteheadi*** Eardley
59b. Body length approximately 4.5-6 mm; whitish vestiture on mesosoma dorsum 60

60a. Dense, white vestiture largely covering tergal discs.....***S. pruinosus*** sp. n.
60b. Vestiture on metasoma not forming thick, frosty bands.....61

61a. Mandibles largely yellow; facial fovea slit-like (bottom not visible).....
.....***S. pyretus*** sp. n.
61b. Mandibles black or dark red-brown; facial fovea narrow but bottom visible .....
.....***S. avius*** Eardley

62a. Ventral margin of clypeus strongly concave, with distinct ventrolateral projections..
.....***S. thoracicus*** (Friese)
62b. Ventral margin of clypeus slightly or not concave, no ventrolateral projections....63

63a. Mesoscutum smooth between punctures 64
63b. Mesoscutum finely reticulate or leathery (coriaceous) between punctures.....72

64a. Claws with basal tooth (careful scrutiny sometimes required) (Fig. W).....65

64b. Claws simple (Fig. X) 67

65a. Basal tomentum along graduli of T2-T5 ..... ***S. tomentum*** Eardley
65b. No basal tomentum on terga 66

66a. Frons smooth between punctures; sculpture in facial fovea smooth .....
..... ***S. capensis*** (Friese)
66b. Frons carinulate between punctures; sculpture in facial fovea finely reticulate.....
..... ***S. leonis*** Cockerell

67a. Wings infuscated ..... ***S. armatipes*** (Friese)
67b. Wings hyaline 68

68a. Metabasitibial plate entire (Fig. T) 69
68b. Metabasitibial plate composed of tubercles or posterior carina only (Fig. S) 71

69a. Pronotal lobe yellow ..... ***S. flavostictus*** Cockerell
69b. Pronotal lobe black 70

70a. Mesoscutum with very sparse punctation ..... ***S. calx*** Eardley
70b. Mesoscutum with fairly dense punctation ..... ***S. catoxys*** sp. n.

71a. Metabasitibial plate comprised of two broad, lanceolate blades and 2-3 apical tubercles; body length >7.5 mm ..... ***S. striatus*** Smith
71b. Metabasitibial plate consisting of posterior carina only; body length <6 mm .....
..... ***S. aureiferus*** Cockerell

72a. Strong posterior white hair-bands on marginal zones of T1-T4 .....
..... ***S. albifumus*** Eardley
72b. No hair-bands along tergal marginal zones 73

73a. Antenna almost completely orange (virtually no black colouring); mesoscutum with fairly dense punctation (interspace approximately 1-1.5X puncture diameter); restricted to savanna areas in northern South Africa and

Zimbabwe ..... ***S. absonus*** Eardley

73b. Antenna orange ventrally, black dorsally; mesoscutum with sparse punctation (interspace >2X puncture diameter); found in Succulent Karoo and Fynbos of western South Africa.....74

74a. Claws toothed; metabasitibial plate not entire consisting of anterior and posterior carinae, posterior carina tuberculate apically .....***S. eremanthedon*** sp. n.

74b. Claws simple; metabasitibial plate entire .....***S. albitarsis*** (Friese)

3.3. Species descriptions

Scrapter acanthophorus sp. n.

Figs 17-21

Etymology: *akantha* (Gr.) = thorn, *phero* (Gr.) = bearer, carrier. In allusion to the distinctive spurred metatibia (Fig. 17).

Holotype ♂: SOUTH AFRICA: *Western Cape*: 30 km north of Vanrhynsdorp (S 31°22'23"S: 18°42'37"E), Knersvlakte, 146 m, 6.ix.2003, K. Timmermann (to be deposited in SANC). Paratypes: 17 ♂♂ collected from the same locality, between 05-11.ix.2003 (MKPC).

Description:

Male.

Measurements (n = 3): head length 1.3 mm, head width 1.7 mm, lower interocular distance 0.9 mm, upper interocular distance 1.1 mm, interantennal distance 0.3 mm, antennocular distance 0.2 mm, length of clypeus 0.4 mm, length of eye 1 mm, width of eye (lateral view) 0.5 mm, width of gena (lateral view) 0.2 mm, length of facial fovea 0.2 mm, maximum width of facial fovea 0.03 mm, mesoscutum length 1 mm, mesosoma length 1.6 mm, forewing length 4.2 mm, length of pterostigma 0.7 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 0.9 mm, length of marginal cell 1.1 mm, length of free-part of marginal cell 0.8 mm.

Vestiture: Clypeus and lower paraocular area with thick, decumbent, bristly, white, plumose setae (underlying integument obscured). Remainder of paraocular area, frons,

scape and vertex with erect, sparse, greyish, plumose setae. Gena with sparse, white, plumose setae. Mesoscutum, scutellum and metanotum covered in sparse, erect, shortish, whitish, plumose setae (integument easily visible). Mes- and metepisterna with long, sparse, white, plumose setae. T2-T5 with bands of white tomentum along graduli. Sterna largely hairless, S4 and S5 with very weak posterior hair-bands, S6 with weak posterior brush of yellowish setae on apical point of sternum.

Integumental colour: Mainly black. Anterior part of protibia and extreme apical end of profemur yellow. Extreme apical end of mesofemur yellow. Antenna ventrally yellow.

Head (Prosoma): Clypeus smooth (except dorsally where finely reticulate) with dense punctation (interspace <0.5X puncture diameter), no clypeal sulcus. Supraclypeal area weakly raised, anterior face of supraclypeal area with weakly reticulated surface and rather sparse punctation (interspace approximately 1.5X puncture diameter). Frontal line carinate. Frons and paraocular area with dense punctation. Facial fovea sulcoid. Ocellar triangle raised in anterior profile. Gena narrower than eye (0.4:1), with heavy punctation and reticulate sculpture. Inner eye orbits diverging dorsally, proportion of lower to upper interocular distance 0.8:1. F1 not elongate. Antenna short, barely reaching tegula.

Mesosoma: Mesoscutum, scutellum and metanotum with fairly dense to dense punctation (interspace 0.5-1X puncture diameter), interspaces shiny and very finely reticulate, median line fairly broad but not deeply impressed, notaulus very weak. Mes- and metepisterna with dense punctation and reticulate interspaces. Propodeum strongly angulate, with dense punctation and rough, reticulate sculpture, propodeal triangle with uniform, rugose sculpture and weak anterior carinae on basal area, margins of triangle pitted.

Metasoma: Tergal discs with finely reticulate sculpture and evenly punctate (interspace 0.5-1X puncture diameter). T2 fovea an elongate ovoid.

Terminalia: Gonobase large, gonoforceps rather narrow, laterally concave, hairy (>30 golden setae), ventrally with transparent membrane, penis valves large, prominent and outer margin ridged (Fig. 18). S6 broadly rounded and hairy posteriorly, anteriorly weakly concave (Fig. 19). S7 weakly concave posteriorly, inconspicuous pointed lateral processes bearing tiny tuft of hair (Fig. 20). S8 posteriorly rounded, posterior region short, very weakly hairy (Fig. 21).

Legs: Metabasitibial plate entire. Claws deeply cleft. Metatibia with pronounced posterior spur (Fig. 17).

Diagnosis: *Scrapter acanthophorus* runs to *S. albitarsis* (Friese) in Eardley's (1996) key, but is substantially larger with much denser scutal punctation and different terminalia (see Eardley 1996, figs 24-26), e.g. *S. acanthophorus* lacks the posterolateral prominences of the S7 found in *S. albitarsis* (Eardley 1996, fig. 24). Further, *S. albitarsis* lacks the black spur on the metatibia characteristic of *S. acanthophorus* (Fig. 17). Several other *Scrapter* species have males with armed hind legs, but they differ substantially from *S. acanthophorus* in general facies. *S. heterodoxus* (Cockerell) is a large, extremely hairy bee, easily distinguished by its strongly swollen metafemur and different terminalia (see Eardley 1996, figs 46-49). *S. armatipes* (Friese) and *S. amplitarsus* (Friese) both differ from *S. acanthophorus* in having swollen metabasitarsi, and in terminalia structure (see Eardley 1996, figs 100-107). *S. aureiferus* Cockerell is a tiny bee (body length 5-6 mm) with bright yellow legs, quite different from *S. acanthophorus*. Finally, *S. acanthophorus* has features suggestive of the *S. nitidus* complex (e.g. raised ocellar triangle, slit-like facial fovea, entire metabasitibial plate and basal pubescence along graduli on T2-T4), but the reticulate mesoscutum, lack of a clypeal sulcus, propodeal triangle largely devoid of carinae and spurred metatibiae easily distinguishes *S. acanthophorus*.

Distribution: Only known from the Knersvlakte, near Vanrhynsdorp, Western Cape. The Knersvlakte is a remarkable region framed in the east by the Bokkeveld Mountains and in the west by the coastal Strandveld. The landscape is one of low, rounded hills and lightly undulating flats covered in white, quartz gravel and pebble fields that give the area a distinctive appearance. The vegetation is sparse, low, dominated by succulents and rich in endemics (Van Wyk & Smith 2001: 52-57). Little is known about the general insect fauna of the Knersvlakte, but endemic flies include the uncommon vermileonid *Leptynoma namaquaensis* (Stuckenberg) and empidid *Edenophorus simplex* Sinclair (Stuckenberg 1996; Sinclair 2002). Furthermore, no fewer than four *Scrapter* species appear endemic to this region viz., *S. acanthophorus*, *S. calx* Eardley, *S. glarea* and *S. sittybon*. This apparent locus of *Scrapter* endemism may be a collecting artifact, and these *Scrapter* species may be found to have a wider distribution with further collecting.

Biology: All specimens have been collected in early September. Several of the paratypes were collected in yellow pan traps. No data on the flower preferences of this species are available.

Scrapter carysomus sp. n.

Figs 22-25

Etymology: *karykrous* (Gr.) = nut-brown; *soma* (Gr.) = body. In reference to the orangish-brown vestiture covering the mesosoma.

Holotype ♂: SOUTH AFRICA: *Northern Cape*: Nieuwoudtville, Farm Glen Lyon (31°24'03"S: 19°08'04"E), 700 m, 30.viii.2003, M. Kuhlmann (to be deposited in SANC). Paratypes: 4 ♂♂from type locality and Nieuwoudtville Flower Reserve collected between 27.viii.2003 and 7.ix.2003 (MKPC).

Description:

Male.

Measurements (n = 1): head length 2 mm, head width 2.3 mm, lower interocular distance 1.6 mm, upper interocular distance 1.6 mm, interantennal distance 0.6 mm, antennocular distance 0.4 mm, length of clypeus 1.8 mm, length of eye 1.5 mm, width of eye (lateral view) 0.5 mm, width of gena (lateral view) 0.6 mm, length of facial fovea 0.4 mm, maximum width of facial fovea 0.1 mm, mesoscutum length 1.3 mm, mesosoma length 2.5 mm, forewing length 6.3 mm, length of pterostigma 1 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 0.8 mm, length of marginal cell 1 mm, length of free-part of marginal cell 0.6 mm.

Vestiture: Generally appears orange-brown when viewed with light microscope. Clypeus with long, white, rather thick, appressed setae. Supraclypeal area, frons, paraocular area and gena sparse (integument easily visible), greyish, erect setae. Scape setae white, long, erect and weakly plumose. Vertex with sparse, yellow-brown, erect setae. Mesoscutum, scutellum and metanotum with sparse (integument easily visible), yellow-brown or orange-brown, erect, weakly plumose setae. Mes- and metepisternum with sparse, weakly plumose, yellow-white setae. Propodeum densely covered (integument obscured) with thick, strongly plumose, erect setae. T1-T5 with short, sparse, inconspicuous white setae on tergal discs, laterally terga with longer white setae; no posterior hair bands on tergal premarginal lines; visible part of T6 disc covered in stout, sub-erect, plumose, black setae. S1 covered throughout in longish, white setae. S2-S6 with sparse, white setae and weak, posterior, white bands.

Integumental colour: Mainly black. Orange-brown patch on anterior side of protibia. Medio- and distitarsus of all legs dark yellow-orange. F1 all black, F2-F11 dorsally black, ventrally yellow-orange, ventral yellow-orange colouring increases in size from tiny dot on F2 to ¾ of flagellomere on F11.

Head (Prosoma): Head robust and 'box-shaped'. Clypeus with dense punctation (interspace 0.5-1X puncture diameter) and finely reticulate sculpture, no clypeal sulcus. Clypeus and

supraclypeal area protuberant. Supraclypeal area anterior face generally smooth, shiny and punctureless (small band of fine reticulation ventrally). Paraocular area, frons and vertex with fairly dense punctation (interspace 0.5-1X puncture diameter). Upper paraocular area, frons and vertex conspicuously carinulate. Frontal line very weak, almost absent. Facial fovea shiny, shallow, ovoid and easily discernable from surrounding integument. Inner eye orbits straight, proportion of lower to upper interocular distance equal. Gena with fairly dense punctation (interspace 0.5-1X puncture diameter) and carinulate, eye slightly narrower than gena (0.8:1). Vertex rounded in anterior profile. F1 elongate. Antenna rather short, reaching tegula.

Mesosoma: Mesoscutum with reticulate sculpture and sparse punctation (interspace 1-2X puncture diameter), median line and notaulus shallowly impressed. Scutellum sculpture similar to mesoscutum, but punctation denser. Metanotum with very dense punctation (interspace <0.5X puncture diameter). Mes- and metepisterna with rough, reticulate surface, almost carinulate over mesepisternum, episternal groove straight, broadly pitted throughout. Propodeum weakly angulate with coarse, velvety black integument, propodeal triangle with irregular carinae on basal area, rugose sculpture between carinae, posteriorly rugose, reticulate pattern, margins of triangle indistinctly pitted.

Metasoma: Tergal discs with finely reticulate sculpture and sparse punctation (interspace >1.5X puncture diameter). T2 fovea ovoid.

Terminalia: Gonoforceps narrowish, tapering posteriorly, hairy, ventrally with transparent membrane, penis valves long and narrow (Fig. 22). S6 medio-posteriorly extended with rear margin slightly concave and hairy, anteriorly strongly concave (Fig. 23). S7 concave and hairy posteriorly (setae yellow, plumose) (Fig. 24). S8 not very hairy, few whitish plumose setae, broadly rounded anteriorly (Fig. 25).

Legs: Metabasitibial plate entire. Claws deeply cleft.

Female: Unknown.

Diagnosis: *Scrapter carysomus* is a medium-sized black bee with noticeable orange-brown mesosomal vestiture and protuberant clypeus. *Scrapter carysomus* is also characterized by its entire metabasitibial plate, reticulate mesoscutum, lack of a clypeal sulcus, punctureless anterior face of supraclypeal area, carinulate vertex and frons. In Eardley's (1996) key, *S. carysomus* exits at *S. niger*, however, *S. carysomus* differs from *S. niger* in deeper concave posterior margin to S7, straighter inner margin to gonocoxite, shorter posterior process to S8, elongate F1, entire metabasitibial plate, slightly shorter wing, and orange-brown

(versus pale yellowish) mesosomal vestiture. These are subtle differences, but collectively they argue for a distinct species. *Scrapter carysomus* is also very similar to *S. capensis* (Friese), particularly in the brownish mesosomal vestiture, but differs in the shape of S8, lacking the deep cleft anteriorly in the disc of *S. capensis* (see Eardley 1996, fig. 96), by lacking the coarsely reticulate mesoscutum of *S. capensis*, by having a protuberant clypeus, in having a weakly angulate propodeum and very different vestiture on S2-3 (lacking the short, plumose setae characteristic of *S. capensis*).

Distribution: Only known from the Nieuwoudtville area, Northern Cape (Succulent Karoo biome).

Biology: Specimens have been collected in Renosterveld from late August to early September, suggestive of an early spring bee. Renosterveld is a fynbos-like shrubland growing on clay-rich soils, and is characterised by the renosterbos (= rhinoceros bush) *Elytropappus rhinocerotis* (L.f.) Less. (Asteraceae). One of the paratypes was collected on an *Oxalis* species (Oxalidaceae).

Scrapter catoxys sp. n.
Figs 26-30

Etymology: *katoxys* (Gr.) = very sharp. In reference to the acute, tapering final black flagellomere of the male antenna (see Fig. V in key) that immediately distinguishes it from other *Scrapter* species, especially *S. calx* Eardley.

Holotype ♂: SOUTH AFRICA: *Northern Cape*: Springbok, Goegap Nature Reserve, hills, 8-10.ix.1992, F.W. and S.K. Gess (AMGS). Paratypes: 2 ♂♂ with same data as holotype (AMGS). Additional material: 3 ♂♂ and 2 ♀♀ with same data as holotype (AMGS).

Description:

Male.

Measurements (n = 3): head length 1.3 mm, head width 1.9 mm, lower interocular distance 0.9 mm, upper interocular distance 1.2 mm, interantennal distance 0.3 mm, antennocular distance 0.3 mm, length of clypeus 0.4 mm, length of eye 1 mm, width of eye (lateral view) 0.6 mm, width of gena (lateral view) 0.2 mm, length of facial fovea 0.3 mm, maximum width of facial fovea 0.06 mm, mesoscutum length 1.2 mm, mesosoma length 2 mm, forewing length 4.3 mm, length of pterostigma 0.6 mm, maximum width of

pterostigma 0.1 mm, length of marginal cell beyond pterostigma 1 mm, length of marginal cell 1.2 mm, length of free-part of marginal cell 0.8 mm.

Vestiture: Hairy bee. Clypeus, supraclypeal area and lower paraocular area with thick, white, decumbent vestiture. Frons and upper paraocular area with erect, thick, white setae. Scape with sparse, white setae. Vertex with sparse, greyish, erect setae. Gena with short, fairly dense, slightly decumbent, white setae. Mesoscutum, scutellum and metanotum with sparse, erect, white setae. Mes- and metepisterna with thick, long, white setae. Propodeum with fairly dense, white setae. Tergal discs with uniform, thick (although integument visible), short, white pubescence. T1-T4 with weak posterior, white, hair-bands along marginal zone. S1 with scattered, inconspicuous white setae. S2-S4 very weak, white, posterior hair-bands.

Integumental colour: Mainly black. Protarsus, protibia and apical end of profemur yellow. Mesotarsus, proximal and apical ends of mesotibia and apical end of mesofemur yellow-orange. Metatarsus, proximal and apical ends of metatibia and apical end of metafemur orange-brown.

Head (Prosoma): Clypeus shiny and smooth with heavy punctation (interspace <0.5X puncture diameter), no clypeal sulcus. Supraclypeal area, frons and paraocular area with dense punctation (interspace <0.5X puncture diameter). Facial fovea sulcoid, elliptical, shiny and smooth. Gena much narrower than eye (0.3:1) with fairly dense punctation. Frontal line weakly carinate. Ocellar triangle raised in anterior profile. Inner eye orbits diverging above, proportion of lower to upper interocular distance 0.8:1. F11 very distinctive, tapering to fine point (see Fig. V in key), antenna moderately long reaching metanotum.

Mesosoma: Mesoscutum smooth and shiny with fairly dense punctation (interspace 0.5-1X puncture diameter), median line weakly impressed, notaulus very weak. Mes- and metepisterna shiny and smooth with heavy punctation (interspace 0.5X puncture diameter), episternal groove pitted throughout. Propodeum angulate and heavily punctate, propodeal triangle shiny, largely smooth with several longitudinal carinae on basal area (weakly or irregularly developed in some specimens), margins of triangle weakly pitted.

Metasoma: Tergal discs smooth and shiny with fairly dense micropunctation. T2 fovea an elongate ovoid.

Terminalia: Gonobase large, gonoforceps curved inwards posteriorly, ventrally membraneous, penis valves narrow, curved inwards (Fig. 26). S6 weakly concave and

hairy posteriorly, weakly concave anteriorly (Fig. 27). S7 essentially truncate posteriorly except for two, very small, black, blunt projections (Fig. 28). S8 posterior disc region short, anteriorly round (Fig. 29).

Legs: Metabasitibial plate near-entire. Claws unusual, pro- and mesopretarsal claws deeply bifid but metapretarsal claws weakly toothed. Metabasitarsus elongate.

Female.

Measurements (n=1): head length 1.4 mm, head width 1.9 mm, lower interocular distance 1.2 mm, upper interocular distance 1.3 mm, interantennal distance 0.3 mm, antennocular distance 0.4 mm, length of clypeus 0.5 mm, length of eye 1 mm, width of eye (lateral view) 0.6 mm, width of gena (lateral view) 0.3 mm, length of facial fovea 0.2 mm, maximum width of facial fovea 0.08 mm, mesoscutum length 1.2 mm, mesosoma length 2 mm, forewing length 4.2 mm, length of pterostigma 0.6 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 1 mm, length of marginal cell 1.2 mm, length of free-part of marginal cell 0.8 mm.

Vestiture: Clypeus sparse, white, bristly setae. White, bristly, fairly long, rather dense setae surrounding antennal sockets. Remainder of face sparsely hairy (setae on vertex with slight gold tinge). Gena rather sparse, white, bristly setae. Mesoscutum sparse, short, white setae, pilosity somewhat thicker on scutellum and metanotum. Sides of mesosoma with rather sparse, white, bristly, long setae. Terga sparse, inconspicuous, white setae throughout disc and weak band of short, white setae along marginal zone. Prepygidial fimbria thick, white, bristly setae. Probasitarsus anteriorly with white, bristly, long setae; posteriorly with brush of short, dense, golden setae. Metatibial scopa completely white. S2 with long, white, plumose setae; S3 thickish band of plumose, white setae posteriorly; remaining sterna with scattered, short setae.

Integumental colour: Mainly black. Protarsus and protibia yellow-orange; mesotibia proximally yellow; terga with brownish tinge.

Head (Prosoma): Clypeus sparsely punctate (interspace approximately 2X puncture diameter), interspaces smooth and shiny. Facial fovea short, shallow ovoid. Supraclypeal area raised, sparsely punctate. Frons and paraocular area densely punctate (interspace <0.5X puncture diameter). Frons and vertex not carinulate. Ocellar triangle raised in anterior profile. Gena smooth and fairly densely punctate. Antenna short, barely reaching tegula. F10 weakly pointed.

Mesosoma: Mesoscutum with dense punctation (interspace <0.5X puncture diameter), interspaces smooth and shiny. Scutellum similar to mesoscutum, but punctation sparse anteriorly. Metanotum with dense punctation. Propodeum angulate; propodeal triangle strikingly smooth and shiny, a few short carinae on basal area. Sides of mesosoma with dense punctation (interspace <0.5X puncture diameter), interspaces smooth and shiny. Episternal groove pitted throughout.

Metasoma: Terga smooth with fairly dense punctation (interspace approximately 1X puncture diameter). T2 fovea elongate ovoid.

Legs: Metabasitibial plate entire, hairy. Claws simple.

Diagnosis: *Scrapter catoxys* is a small, shiny, hairy, black bee (Fig. 30); the metasomal tergal discs are noticeably covered throughout in fairly thick, white vestiture. Superficially, it resembles other hylaeiform *Scrapter* species, but the acutely pointed F11 is distinctive (see Fig. V in key). In particular, *S. catoxys* resembles *S. calx*, but the colouration and structure of the antennae are different, the acute F11 being especially diagnostic of *S. catoxys*. Further, the gonostylus of *S. catoxys* lacks an expanded inner margin (present in *S. calx*), the S7 of *S. catoxys* lacks posterolateral processes (present in *S. calx*) and the metadistitarsi are elongate (not elongate in *S. calx*). The ranges of *S. calx* and *S. catoxys* also appear allopatric (*S. calx* is seemingly largely circumscribed to the Knersvlakte).

Distribution: Only known from Goegap Nature Reserve, approximately 12 km east of Springbok (Succulent Karoo biome).

Biology: Flight period is September to October. The type series was collected on *Cotula barbata* DC. (Asteraceae), which is a small, wiry annual bearing yellow, umbel-shaped flowers and is widespread in Namaqualand.

Scrapter chrysomastes sp. n.
Figs 31-35

Etymology: *chryso* (Gr.) = gold, *mastix* (Gr.) = whip. In reference to the diagnostic, largely yellow, remarkably long, whip-like antennae (Fig. 31).

Holotype ♂: SOUTH AFRICA: *Northern Cape*: Richtersveld National Park, between hills at 28°08'S: 17°01'E, northwest of Koeroegabvlakte, 14.ix.1996, F.W., S.K. and R.W. Gess (AMGS). Paratypes: 3 ♂♂, same data as holotype (AMGS).

Description:

Male.

Measurements (n = 1): head length 1.3 mm, head width 1.6 mm, lower interocular distance 1 mm, upper interocular distance 1 mm, interantennal distance 0.3 mm, antennocular distance 0.3 mm, length of clypeus 0.4 mm, length of eye 0.5 mm, length of facial fovea 0.3 mm, maximum width of facial fovea 0.03 mm, width of eye (lateral view) 0.5 mm, width of gena (lateral view) 0.3 mm, mesoscutum length 1.1 mm, mesosoma length 2 mm, forewing length 4.2 mm, length of pterostigma 0.6 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 1 mm, length of marginal cell 1.1 mm, length of free-part of marginal cell 0.6 mm.

Vestiture: Overall, rather sparse, bright white vestiture including white metasomal hairbands. Clypeus with thick, short, starkly white, decumbent setae. Supraclypeal area, frons and lower paraocular area with short, erect, white setae. Scape setae white and bristly. Vertex with sparse, erect, long, whitish setae. Gena with white, fairly dense setae. Mesoscutum with very sparse, erect, white vestiture. Scutellum and metanotum covered in sparse, white setae. Mesepisternum with sparse, white setae. Mesosoma ventrally with thick, white, decumbent vestiture. Propodeum with sparse, white vestiture. Tergal discs with very sparse, erect, white setae. T1-T4 with decumbent, white hair-bands along marginal zones (hair-bands easily discernable with naked eye). T5 with very weak hair-band. S2 with long, shaggy, fairly sparse, white setae. S3-S6 hairiness declines progressively, S5 and S6 mostly hairless.

Integumental colour: Black except for bright yellow protibia, protarsi and apical part of profemur, middle leg the same, hindleg similar but patch of dark red-brown medially on metatibia; mandibles yellow except for dark apical ends; underside of antenna from pedicel to F9 yellow.

Head (Prosoma): Clypeus shiny with heavy punctation (interspace <0.5X puncture diameter), no clypeal sulcus. Supraclypeal area flat (no anterior face of supraclypeal area), abundant deep punctures. Paraocular area and frons with fine, reticulate sculpture and heavy punctation. Vertex similar sculpture to paraocular area but less heavily punctured. Ocellar triangle raised in anterior profile. Frontal line weakly carinate. Facial fovea narrow, shallow and inconspicous. Gena shiny, narrower than eye (0.6:1) with moderate punctation and weakly carinulate. Inner eye orbits straight, proportion of lower to upper interocular distance equal. Antenna all segments long and cylindrical, each segment similar in length, antenna long, extending to metasomal terga (Fig. 31).

Mesosoma: Mesoscutum and scutellum shiny with fine, reticulate sculpture and very sparse punctation (interspace >2X puncture diameter), punctures irregularly clumped, large areas of mesoscutum punctureless, median line and notaulus weakly impressed. Metanotum with roughened sculpture and few punctures. Mes- and metepisternum with fine reticulate sculpture and very sparse punctation, episternal groove straight, weakly pitted especially in upper part of groove. Propodeum strongly angulate, with shiny, roughened sculpture, propodeal triangle with roughened, complex patterning and weak, irregular network of carinae on basal area, margins of triangle barely pitted.

Metasoma: Tergal discs with fine, reticulate sculpture and very sparse punctation (interspace 2X puncture diameter). T2 fovea ovoid.

Terminalia: Gonoforceps narrow, inner margin tapering posteriorly, ventrally membraneous, penis valves narrow (Fig. 32). S6 posteriorly concave, tufts of setae on rear margin of posterior lobes, anteriorly weakly concave (Fig. 33). S7 concave posteriorly forming two, fairy acute, hirsute points (Fig. 34). S8 posterior disc process short, quite hairy, anteriorly truncate (Fig. 35).

Legs: Metabasitibial plate not entire, only posterior carina present. Claws cleft.

Female: Unknown.

Diagnosis: *Scrapter chrysomastes* is one of the most striking species in the genus due to the extremely long antennae (Fig. 31). When fully extended the apices of the antennae reach tergum 3. These very long, whip-like antennae immediately distinguish *S. chrysomastes* from all other known *Scrapter* species, and the feature can easily be seen with the naked eye.

Distribution: Only known from the Richtersveld, Northern Cape. The Richtersveld is an arid, rugged region that is renowned for its botanical endemism (Van Wyk & Smith 2001: 38-43). Increasingly, entomologists are paying closer attention to its largely endemic insect fauna (e.g. Stuckenberg 1998). *Scrapter chrystomastes* appears to be another notable Richtersveld endemic, although the plant it was collected on is fairly widespread in Namaqualand.

Biology: The type series was collected in mid-September on *Roepera foetida* Sond. (Zygophyllaceae). This shrub bears yellow or white flowers and is known as the skilpadbos (= tortoise bush). It is common in the rocky hills of the Namaqualand escarpment.

Scrapter eremanthedon sp. n.

Figs 36-39

Etymology: *eremia* (Gr.) = desert, wilderness, *anthedon* (Gr.) = bee.

Holotype ♂: SOUTH AFRICA: *Northern Cape*: Nieuwoudtville, Farm Glen Lyon (31°24'03"S: 19°08'34"E), 700 m, 27.viii.2003, M. Kuhlmann (to be deposited in SANC). Paratypes: 2 ♀♀ collected in Nieuwoudtville area between 23.viii.2003 and 27.viii.2003 (MKPC).

Description:

Male.

Measurements (n = 1): head length 1.8 mm, head width 2.2 mm, lower interocular distance 1.4 mm, upper interocular distance 1.4 mm, interantennal distance 0.4 mm, antennocular distance 0.4 mm, length of clypeus 0.4 mm, length of eye 1.3 mm, width of eye (lateral view) 0.7 mm, width of gena (lateral view) 0.4 mm, length of facial fovea 0.4 mm, maximum width of facial fovea 0.1 mm, mesoscutum length 1.2 mm, mesosoma length 2.3 mm, forewing length 5.7 mm, length of pterostigma 1 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 1.3 mm, length of marginal cell 1.6 mm, length of free-part of marginal cell 1 mm.

Vestiture: Clypeus with thick, white, appressed, weakly plumose setae. Supraclypeal area, frons and paraocular area with erect, plumose grey setae. Scape setae sparse, white, erect and weakly plumose. Vertex with tall, greyish, plumose setae, about five black plumose setae intermixed. Gena ventrally with long, weakly plumose, white setae. Mesoscutum, scutellum and metanotum covered in sparse (integument easily visible), whitish, plumose setae with a few black, plumose setae intermixed. Mes- and metepisterna covered in fairly sparse, long, white, plumose setae. Propodeum sparsely covered in greyish, plumose setae (integument easily visible). T1-T5 discs covered in sparse, inconspicuous, short, whitish setae, no posterior hair bands; visible part of T6 covered in long, plumose, mainly black bristles. Sterna covered sparsely in long, white, plumose setae, no posterior hair bands.

Integumental colour: All black except that flagellomeres slightly paler ventrally (but no orange or yellow colouring).

Head (Prosoma): Clypeus protuberant and shiny with fairly dense punctation (interspace approximately 1X puncture diameter), punctation denser on apical edge (interpsace

approximately 0.5X puncture diameter), integument finely reticulate between punctures; no clypeal sulcus. Supraclypeal area raised, anterior face of supraclypeal area shiny with fine reticulate sculpture. Paraocular area with roughened, near-carinulate sculpture. Frontal line carinate. Frons with roughened, almost carinulate sculpture. Facial fovea ovoid, smooth and easily discernable from surrounding integument. Inner eye orbits straight, proportion of lower to upper interocular distance equal. Vertex with roughened sculpture, but not carinulate, rounded in anterior profile. Gena weakly carinulate and narrower than eye (0.6:1). F1 slightly elongate. Antenna long, reaching scutellum.

Mesosoma: Mesoscutum and scutellum with shiny, reticulate sculpture and fairly dense punctation (interspace 1X puncture diameter), median line and notaulus shallowly impressed. Metanotum with rough, reticulate sculpture and sparse punctation. Mes- and metepisterna with dense reticulate sculpture, episternal groove arced forward, pitted throughout. Propodeum strongly angulate, propodeal triangle basal area almost horizontal, weak longitudinal carinae on basal area, remainder of triangle with uniform, roughened, reticulate pattern, margins of triangle not pitted.

Metasoma: All tergal discs with uniform, finely reticulate reticulate sculpture. T1-T5 with sparse micropunctation (interspace >2X puncture diameter). T6 with denser punctation (interspace 0.5-1X puncture diameter), punctures also larger. T2 fovea an indistinct ovoid.

Terminalia: Gonobase large, gonoforceps hairy posteriorly, ventrally membraneous, penis valves narrow (Fig. 36). S6 posteriorly weakly concave, tufts of hair on rear margin of posterior lobes, anteriorly strongly concave (Fig. 37). S7 concave posteriorly, hirsute posterolaterally (Fig. 38). S8 glued to card, anterior region not discernable, rounded and very hairy posteriorly (Fig. 39).

Legs: Metabasitibial plate near-entire with anterior tooth. Claws deeply bifi

Female.

Measurements (n = 2): head length 1.9 mm, head width 2.3 mm, lower inte ;ular distance 1.6 mm, upper interocular distance 1.5 mm, interantennal distance 0.4 m antennocular distance 0.5 mm, length of clypeus 0.6 mm, length of eye 1.4 mm, widtl ·f eye (lateral view) 0.7 mm, width of gena (lateral view) 0.3 mm, length of facial fovea 0.4 mm, maximum width of facial fovea 0.1 mm, mesoscutum length 1.4 mm, mesosoma length 2.5 mm, forewing length 6 mm, length of pterostigma 0.9 mm, maximum width of pterostigma 0.3 mm, length of marginal cell beyond pterostigma 1.2 mm, length of marginal cell 1.5 mm, length of free-part of marginal cell 0.9 mm.

Vestiture: Clypeus and lower paraocular area with sparse, sub-erect, plumose yellow-white setae. Scape, frons, upper supraclypeal area and upper paraocular area with fairly dense, erect, plumose greyish setae. Vertex covered in sparse, erect, whitish plumose setae (varying in length) and interspersed with several erect, black setae. Gena sparsely hairy except ventrally where long, downward-projecting, plumose setae present. Mesoscutum covered in sparse, short, yellow-white, plumose setae with some black setae intermixed. Scutellum and metanotum similar to mesoscutum, but setae denser and more orange. Mesepisternum sparsely covered in white, plumose setae but ventrally vestiture thicker. Propodeum with fairly dense, yellowish, erect, plumose setae. T1 and T2 very sparsely pubescent (superficially appear hairless), except laterally where fairly dense, sub-erect, plumose white setae present. T3 and T4 appear hairless but covered in many, tiny, inconspicuous, short, white setae. T5 prepygidial fimbria consists of dense, sub-erect, plumose, stout, black setae. S2-S5 with sparse, sub-erect, whitish plumose setae. Probasitarsus with anterior brush of golden, simple, distally-projecting setae, posteriorly with thick, stiff-haired golden brush. Metatibial scopa anteriorly with long, white, palmate setae, dorso-posteriorly with ridge of black, plumose, stout setae, and posteriorly with longish, straight, white, simple keirotrichia.

Integumental colour: All black except F10-F11 ventrally dull orange.

Head (Prosoma): Clypeus protuberant with finely reticulate sculpture and fairly dense punctation (0.5-1X puncture diameter interspace), no clypeal sulcus. Supraclypeal area raised, anterior face of supraclypeal area shiny, largely punctureless with finely reticulate sculpture. Paraocular area with reticulate sculpture and dense punctation (0.5X puncture diameter interspace). Upper paraocular area, frons and vertex distinctly carinulate. Frontal line barely carinate. Facial fovea shallow, smooth, elongate ovoid and easily discernable from surrounding integument. Gena narrower than eye (0.4:1), with reticulate sculpture and fairly dense punctation. Inner eye orbits straightish, proportion of upper to lower interocular distance 0.9:1. Vertex rounded in anterior profile. F1 slightly elongate.

Mesosoma: Mesoscutum with reticulate sculpture and sparse punctation (approximately 2X puncture diameter interspace), median line moderately impressed, quite broad, notaulus very weak. Scutellum and metanotum similar sculpture to mesoscutum but punctation denser. Mesepisternum with roughened sculpture, almost carinulate, episternal groove arced forward and weakly pitted. Propodeum angulate, with shiny, reticulate sculpture, propodeal triangle with uniform, reticulate pattern lacking carinae, margins of triangle not pitted.

Metasoma: Tergal discs with fine, reticulate sculpture and sparse, tiny punctures. T5 with denser, larger punctures. T2 fovea a broad ovoid.

Legs: Metabasitibial plate composed of two carinae (anterior and posterior), posterior carina tuberculate apically. Claws weakly cleft.

Diagnosis: *Scrapter eremanthedon* is an all-black bee, including the ventral sides of the antennae (orangish in female). In Eardley's (1996) key, the male comes to *S. niger*, but differs from that species in the protuberant clypeus, reticulate mesoscutum, less dense scutal punctation, strongly angulate propodeum and fairly elongate F1. The female is identified by the reticulate sculpture, sparse mesoscutal punctation, carinulate vertex, lack of a clypeal sulcus, lack of tergal hair bands, distinctly orange-brown vestiture of mesosoma, angled propodeum and uniformly reticulate propodeal triangle, non-entire metabasitibial plate and protuberant clypeus. The female resembles the female of *S. niger*, but lacks the clypeal tubercle and has bifid not simple claws.

Distribution: Only known from the Nieuwoudtville area, Northern Cape (Succulent Karoo biome).

Biology: Specimens have been collected in late August, at the beginning of the austral spring. Specimens have been taken on an *Oxalis* species (Oxalidaceae).

Scrapter glarea sp. n.
Figs 40-43

Etymology: *glarea* (L.) = gravel. A noun in apposition, in reference to the type locality, the Knersvlakte, an area characterised by its quartz gravel fields.

Holotype ♂: SOUTH AFRICA: *Western Cape*: 30km N Vanrhynsdorp (31°22'23"S: 18°42'37"E), Knersvlakte, 146 m, 5.ix.2003, K. Timmermann (to be deposited in SANC). Paratype: 1♂ from type locality collected on 29.ix.2003 (MKPC).

Description:

Male.

Measurements (n = 2): head length 1.3 mm, head width 1.5 mm, lower interocular distance 0.8 mm, upper interocular distance 1.1 mm, interantennal distance 0.4 mm, antennocular distance 0.2 mm, length of clypeus 0.5 mm, length of eye 1 mm, width of eye (lateral

view) 0.4 mm, width of gena (lateral view) 0.3 mm, length of facial fovea 0.2 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 0.9 mm, mesosoma length 1.7 mm, forewing length 4.1 mm, length of pterostigma 0.7 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 0.9 mm, length of marginal cell 1.1 mm, length of free-part of marginal cell 0.7 mm.

Vestiture: Clypeus, lower paraocular area and supraclypeal area with long, thick, weakly plumose, decumbent white setae (integument obscured). Upper paraocular area, frons and vertex with sparse, erect, whitish setae. Scape with sparse, whitish setae. Gena with sparse, whitish, weakly plumose setae. Mesoscutum covered in sparse, erect, rather short, whitish, plumose vestiture. Scutellum and metanotum similar to mesoscutum but setae light orange-brown. Sides of mesosoma with long, white, plumose setae. T2-T4 (but more T2-T3) with dense, short, decumbent, white pubescence on anterior part of tergal discs, T5 sparse, whitish, short setae, T1 largely hairless. Sterna largely hairless.

Integumental colour: Mainly black. Antenna ventrally yellow. Protibia yellow (but with dark brown patch posteriorly), extreme apical end of profemur also yellow. Apical end of mesofemur, -tibia (except for posterior brown patch) and -tarsus yellow. Hindleg resembles middle leg.

Head (Prosoma): Clypeus smooth with dense punctation (interspace 0.5X puncture diameter), no clypeal sulcus. Supraclypeal area raised, anterior face of supraclypeal area largely impunctate (interspace >3X puncture diameter) and smooth. Frontal line weakly carinate. Frons and upper paraocular area carinulate. Facial fovea sulcoid and inconspicuous. Ocellar triangle raised in anterior profile. Gena slightly narrower than eye (0.8:1), fairly densely punctate and finely reticulate. Inner eye orbits diverging dorsally, proportion of lower to upper interocular distance 0.7:1. F1 not elongate. Antenna quite long, reaching metanotum.

Mesosoma: Mesoscutum with fine, reticulate sculpture and sparse punctation (interspace >2X puncture diameter), median line weakly impressed, notaulus very weak. Scutellum and metanotum sculpture similar to mesoscutum but punctation denser. Mes- and metepisterna with rough, reticulate sculpture and fairly dense punctation, episternal groove straight, pitted throughout. Propodeum angulate with roughened reticulation and fairly dense punctation, propodeal triangle with uniform, reticulate sculpture and weak anterior carinae on basal area.

Metasoma: T1-T5 discs with finely reticulate sculpture. T2-T4 with dense micropunctation on anterior part of discs, remainder of discs impunctate. T5 with more evenly spaced macropunctation. T2 fovea an elongate ovoid.

Terminalia: Gonobase large, gonoforceps margins smooth and largely parallel, rounded posteriorly, hirsute, ventrally with transparent membrane, penis valves narrow, ending in acute point (Fig. 40). S6 large in relation to S7 and S8, weakly concave posteriorly with hairy posterior margin to lobes, strongly concave anteriorly (Fig. 41). S7 concave posteriorly, hirsute posterolaterally (Fig. 42). S8 posterior disc with hind margin truncate, posteriorly fairly hairy, anteriorly rather rounded (Fig. 43).

Legs: Metabasitibial plate entire in holotype, but only posterior carina visible in paratype. Claws deeply cleft.

Female: Unknown.

Diagnosis: *Scrapter glarea* is an elongate, small bee characterised by its lack of a clypeal sulcus, inconspicuous, sulcoid facial fovea, raised ocellar triangle, starkly yellow tibiae and tarsi and leathery mesoscutum with reduced punctation. The S7 recalls *S. niger*, but *S. glarea* is smaller, and differs in the features mentioned above, especially in having reduced mesoscutal punctation, and also in having a truncate hind margin to S8.

Distribution: Only known from the Knersvlakte, near Vanrhynsdorp, Western Cape (Succulent Karoo biome). See comments under *S. acanthophorus* regarding this region.

Biology: Type series collected in September. No pollen/nectar source data.

Scrapter oxyaspis sp. n.
Figs 44-48

Etymology: *oxys* (Gr.) = sharp or pointed, *aspis* (Gr.) = shield. In reference to the distinctive, sharp point on the posterior margin of S7 (Fig. 46).

Holotype ♂: SOUTH AFRICA: *Northern Cape*: Nieuwoudtville, Farm Glen Lyon (31°24'03"S: 19°08'34"E), 7.ix.2003, M. Kuhlmann. (to be deposited in SANC). Only known from holotype.

Description:

Male.

Measurements (n = 1): head length 1.9 mm, head width 2.5 mm, lower interocular distance 1.3 mm, upper interocular distance 1.7 mm, interantennal distance 0.4 mm, antennocular distance distance 0.4 mm, length of clypeus 0.6 mm, length of eye 1.5 mm, length of facial fovea 0.5 mm, maximum width of facial fovea 0.08 mm, width of eye (lateral view) 0.6 mm, width of gena (lateral view) 0.5 mm, mesoscutum length 1.6 mm, mesosoma length 2.4 mm, forewing length 7 mm, length of pterostigma 1.1 mm, maximum width of pterostigma 0.3 mm, length of marginal cell beyond pterostigma 1.6 mm, length of marginal cell 1.9 mm, length of free-part of marginal cell 1.1 mm.

Vestiture: Almost entirely white. Head very hairy and underlying integument difficult to discern. Clypeus entirely covered by thick, long, starkly white, weakly plumose, decumbent setae. Paraocular area, supraclypeal area and frons with erect, greyish, plumose setae. Scape setae long, sparse, white and plumose. Vertex with sparse, long, grey, erect, plumose setae. Gena with shortish, white setae. Mesosoma appears very woolly. Mesoscutum covered with thick, flowing, long, white, plumose setae but underlying integument easily visible. Scutellum and metanotum resembling mesoscutum but proximal third of setae dark. Mesepisternum sparsely covered in long, grey, plumose setae but becoming much denser and whiter ventrally. Metepisternum and propodeum with sparse, long, grey setae. All terga lack posterior hair bands, each disc on T1-T5 with long, erect, white, plumose setae (but underlying integument clearly visible), marginal zones of terga with weak, sub-erect, white setae, T6 with much shorter setae on disc and longer, black (not white) setae on marginal zone. S2 and S3 with posterior third covered in long, appressed, white setae, other sterna less hairy, S5 and S6 almost hairless.

Integumental colour: All black (including mandibles), no trace of yellow or red-brown colouration except claws proximally yellow and flagellomeres ventrally dark brown.

Head (Prosoma): Clypeus with dense punctation (interspace <0.5X puncture diameter), no clypeal sulcus. Supraclypeal area raised, anterior face of supraclypeal area shiny and punctureless with finely reticulate pattern. Frontal line barely carinate. Inner eye orbits diverging slightly dorsally, proportion of lower to upper interocular distance 0.8:1. Paraocular area and frons densely punctate (interspace <0.5X puncture diameter). Frons and vertex heavily carinulate. Facial fovea irregular ellipsoid, weakly differentiated from surrounding integument. Gena heavily punctate (interspace 0.5-1X puncture diameter), and slightly narrower than eye width (0.8:1). Vertex rounded in anterior profile. F1 not elongated. Antenna long reaching scutellum.

Mesosoma: Mesoscutum with moderate punctation (interspace 1-1.5X puncture diameter) and shiny, finely reticulate interspaces, median line and notaulus weakly impressed. Scutellum sculpture and punctation similar to mesoscutum. Mes- and metepisternum with finely reticulate sculpture, episternal groove arced forward, pitted except near top of groove. Propodeum weakly declivitous, propodeal triangle dull with uniform, reticulate pattern, anterior carinae on basal area very weak, margins of triangle indistinctly pitted.

Metasoma: Tergal discs with finely reticulated integument and moderate punctation (interspace 1-1.5X puncture diameter); T1 anterior, mediolongitudinal groove present; T2 fovea elliptical.

Terminalia: Gonobase large, gonoforceps posteriorly hairy (>20 golden plumose setae), ventrally membraneous, penis valves narrow (Fig. 44). S6 posteriorly concave, tuft of setae on rear margin of posterior lobes, anteriorly strongly concave (Fig. 45). S7 posteriorly terminating in fine, sharp point, rear margin of sternum also hairy (setae erect, yellow and plumose) (Fig. 46). S8 posteriorly blunt-tipped, very hairy (setae erect, yellow and plumose), S8 glued to card and anterior portion not discernable (Fig. 47).

Legs: Metabasitibial plate entire. Claws deeply cleft.

Female: Unknown.

Diagnosis: *Scrapter oxyaspis* is a medium-sized, all black, very hairy bee (Fig. 48). It is characterized by its lack of any yellow integument, leathery mesoscutum, structure of the genitalia and S7, shiny, punctureless anterior face of supraclypeal area, weakly developed facial fovea, no clypeal sulcus, entire metabasitibial plate, very hairy mesosoma and uniformly patterned propodeal triangle. In Eardley's (1996) key, *S. oxyaspis* exits at *S. striatus* Smith, but differs from that species in the shape of the terminalia (Figs 44-47), facial fovea (distinct in *S. striatus*), propodeal triangle sculpture (*S. striatus* has conspicuous carinae), shiny unpunctured supraclypeal area and lack of yellow on the legs. Superficially, *S. oxyaspis* recalls *S. tomentum* Eardley, but differs strongly from this species in lacking the distinctive flagellomere colour pattern and flat supraclypeal area of *S. tomentum*. Furthermore the terminalia are quite different (e.g. *S. tomentum* S7 is concave posteriorly). *Scrapter oxyaspis* also resembles *S. capensis*, but the S7 of *S. oxyaspis* is distinct and the holotype lacks the brownish vestiture of the mesoscutum and scutellum that is characteristic of *S. capensis*.

Distribution: Only known from the Nieuwoudtville area, Northern Cape (Succulent Karoo biome).

Biology: The holotype was collected in early September, suggesting *S. oxyaspis* is an early spring bee. The holotype was collected in Renosterveld on an *Oxalis* species (Oxalidaceae).

Scrapter pruinosus sp. n.

Figs 49-57

Etymology: *pruinosus* (L.) = frosty, covered in hoar-frost or ice. In allusion to the characteristic vestiture of this bee that affords it a frosty appearance (Figs 49-51).

Holotype ♂: NAMIBIA: Lüderitz (26°35'S:15°07'E), 7.xii.1994, M. Kuhlmann (SANC). Paratypes: 11 ♂♂ and 10 ♀♀ with same data as the holotype (all MKPC, except 1 ♀ in SANC).

Description:

Male.

Measurements (*n*=4): total body length 5.9 mm, head length 1.5 mm, head width 1.8 mm, lower interocular distance 1 mm, upper interocular distance 1.3 mm, interanntenal distance 0.4 mm, antennocular distance 0.2 mm, length of clypeus 0.6 mm, length of eye 1.2 mm, length of facial fovea 0.4 mm, maximum width of facial fovea 0.04 mm, mesoscutum length 1 mm, mesosoma

length 2 mm, forewing length 3.9 mm, length of pterostigma 0.6 mm, maximum width of pterostigma 0.1 mm, length of marginal cell beyond pterostigma 0.8 mm, length of marginal cell 1.1 mm, length of free-part of marginal cell 0.7 mm, metatibia length 1.2 mm, metabasitarsus length 0.7 mm.

Vestiture: With the naked eye, the frosty-white, short vestiture is immediately striking and distinctive. Clypeus, supraclypeal area and lower paraocular areas completely obscured by

dense, white, decumbent, minutely plumose ('bristly') setae. Frons, vertex, upper paraocular area with sparse, erect, white setae (integument easily discernable). Mesoscutum, scutellum and metanotum thickly covered in short, decumbent to sub-erect, short, stout, bristly setae. Sides of mesosoma with fairly dense, white, bristly vestiture. Tergal discs thickly covered in short, dense, decumbent, bristly, white setae, most of integument not visible. T6 and T7 setae longer and more golden. Sternal discs have very sparse, longish setae (contrasting notably with tergal vestiture).

Integumental colour: Principally black bar metasoma and legs. Protibia and protarsi bright yellow (protibia with pale brownish patch anteriorly). Distal end of profemur orange-yellow. Mid- and hind-leg with similar colour pattern. Antenna brownish above, bright yellow below (on F2-F5 dorsal brown patches reduced, most of flagellomere yellow). Mandibles distally black, basal 2/3 yellow. T1, T2 and T3 posterior band along marginal zone orange-red, remainder of tergal segment black. T4 and T5 mainly black. All sterna orange-yellow.

Head (Prosoma): Clypeus heavily punctate (interspace <0.5X puncture diameter), narrow interspaces smooth and shiny, no medio-longitudinal clypeal sulcus, ventral magin of clypeus slightly emarginate. Supraclypeal area weakly elevated with dense punctation. Frontal line barely evident. Facial fovea sharply-defined, narrow, shiny and smooth. Paraocular area and frons densely punctate. Inner eye orbits diverging dorsally, proportion of lower to upper interocular distance 0.8:1. Antenna rather short, just reaching tegula. Labrum longer than broad. Basal area of labrum smooth and elevated with medial protuberance, distal area of labrum hairy.

Mesosoma: Lateral ridge of pronotum not strongly elevated but narrow-edged. Oblique lateral sulcus of pronotum well-developed, terminating dorsad of pronotal ridge. Mesoscutum heavily punctate (interspace <0.5X puncture diameter), narrow interspaces smooth and shiny. Median line moderately impressed, notaulus barely evident. Scutellum and metanotum sculpture similar to mesoscutum. Propodeum angulate. Propodeal triangle basal area with sharply-defined, irregular, mostly longitudinal carinae; interspaces roughened. Mesepisternum smooth, shiny and densely punctate (interspace <0.5-1X puncture diameter). Pre-episternal groove strongly impressed, pitted throughout.

Metasoma: Tergal discs smooth, shiny and densely punctate. T2 fovea ovoid. Pygidial plate absent.

Terminalia: Gonobase large, inner margin of gonocoxite toothed, gonoforceps divided into two surfaces by medial, longitudinal ridge; outer surface concave and moderately hairy, inner surface undistinguished, rather flat with few setae (Fig. 52). Penis valves long, narrow and slightly exceeding gonoforceps in length (Fig. 52). Ventrally gonoforceps with large ventral process (Fig. 52). Well-defined digitus and cuspis in volsella (Fig. 52). S6 weakly emarginate posteriorly with broad field of setae (Fig. 53). S7 simple in form, weakly emarginate posteriorly forming two points (Fig. 54). S8 posterior region elongate, posterior plate sub-truncate, posterior process fairly hairy (Fig. 55).

Legs: Metabasitibial plate only with posterior carina present. Pretarsal claws deeply cleft.

Female.

Measurements (n=4): total body length 6.9 mm, head length 1.7 mm, head width 2.1 mm, lower interocular distance 1.3 mm, upper interocular distance 1.4 mm, interanntenal distance 0.4 mm, antennocular distance 0.4 mm, length of clypeus 0.6 mm, length of eye 1.3 mm, length of facial fovea 0.6 mm, maximum width of facial fovea 0.03 mm, mesoscutum length 1.2 mm, mesosoma length 2.3 mm, forewing length 4.5 mm, length of pterostigma 0.7 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 1.0 mm, length of marginal cell 1.2 mm, length of free-part of marginal cell 0.7 mm, metatibia length 1.4 mm, metabasitarsus length 0.9 mm.

Vestiture: Generally similar to ♂. Face thick, white, bristly setae (especially dense on paraocular area and frons). Vertex sparse, erect, white setae. Gena dense, appressed, bristly, white setae (integument largely obscured). Mesoscutum, scutellum and metanotum thickly covered in short, erect, bristly setae (integument not completely obscured, though). Sides of mesosoma similar but longer, sparser setae. Metasomal terga with very dense, white, short, bristly vestiture largely obscuring integument. S1 and S2 with long, plumose, white setae forming fairly thick scopa. Remaining sterna with a few plumose setae, but vestiture weak. Sparse brush on anterior (outer) surface of probasitarsus composed of simple and branched setae. Metatibial scopa and prepygidial fimbria all white.

Integumental colour: Mainly black, posterior third of T1-T5 bright orange. S2-S4 orange, S5-S6 dark orange-brown. All tibia and tarsi yellow-orange, but metadistitarsus dark orange-brown. Apex of pro- and mesofemur yellow-orange. Undersides of antenna yellow.

Head (Prosoma): Clypeus smooth, shiny, dense punctation (interspace about 0.5X puncture diameter), no medio-longitudinal clypeal sulcus. Supraclypeal area weakly elevated with dense punctation. Paraocular area and frons dense punctation, smooth interspaces. Facial fovea narrow and smooth. Labrum longer than broad, elevated basal zone with medial protuberance. Glossa apex weakly emarginate. Galeal comb comprising approximately 12 teeth. Maxillary palp slightly exceeding galeal apex in length (last two palpomeres protruding).

Mouthparts: Weakly bilobed glossa with strong glossal brush. Maxillary palp quite long, slightly exceeding galea apex. Labial palp short, falling short of glossa apex.

Mesosoma: Lateral ridge of pronotum rather weakly developed, narrow-edged. Oblique lateral sulcus of pronotum well-developed, terminating dorsad of pronotal ridge. Mesoscutum fairly dense to dense punctation (interspace about 0.5-1X puncture diameter). Scutellum and metanotum similar mesoscutum. Mes- and metepisterna fairly dense to dense punctation, smooth interspaces. Propodeum angulate. Propodeal triangle basal area with longitudinal carinae and roughened interspaces.

Legs: Metabasitibial plate reduced to very short, posterior carina proximally and about 6 small tubercles delineating outline of plate (Fig. 56). Pretarsal claws deeply cleft, pre-apical tooth slightly shorter than outer tooth (Fig. 57).

Terminalia: T7 with strongly produced apodemal region, posterior edge straightish, spiracle placed far back but not opening onto posterior edge, lateral lamina narrow (approximately 0.1X breadth of lamina spiracularis). Dorsal arm of furcula approximately 0.5X length of ventral arm. Apodemal ridge of 2nd gonocoxa straight. Gonoplac parallel-sided, hairy distally.

Diagnosis: A tiny bee characterised by its distinctive 'hoar-frost' vestiture, yellowish mandibles, bright yellow legs, and partially red T1-T3. Further features include fairly dense (♀) to very dense (♂) mesoscutum punctation, lack of a clypeal sulcus, tuberculate metabasitibial plate (♀), deeply cleft claws and narrow facial foveae (bottom of fovea visible). The ♂ *S. pruinosus* is strikingly similar to *S. avius* but the dense metasomal vestiture is diagnostic, the terminalia are distinct (see Eardley 1996: figs 32-34 for *S. avius*) and *S. avius* does not have a reddish metasoma. The ♀ *S. pruinosus* is also similar to *S. avius*, but the thick, white vestiture on the mesoscutum and metasoma of *S. pruinosus* is distinctive. Further T2-T4 is all orange in *S. avius* but banded black and orange in *S. pruinosus*, and the prepygidial fimbria in *S. avius* has some black setae (all white in *S. pruinosus*).

Distribution: *S. pruinosus* is only known from the type locality of Lüderitz, which is a town at sea-level in southern Namibia. The Lüderitz area is a harsh, hyper-arid environment with cold buffeting Atlantic winds and a sparse, dwarf shrubland vegetation. Lüderitz falls near the northern edge of Succulent Karoo biome (and winter rainfall zone).

Biology: There are no relevant floral records.

Scrapter pyretus sp. n.

Figs 58-62

Etymology: *pyretos* (Gr.) = burning hot, fiery. In allusion to the sweltering type locality in Namibia, and the fiery orange metasoma in both sexes.

Holotype ♂: NAMIBIA: Gaub Pass (23°30'S:15°46'E), 19.iii.1997, F.W. & S.K. Gess (AMGS). Paratypes: 6 ♂♂ and 4 ♀♀ with same data as holotype (AMGS), and 7 ♂♂ and 8 ♀♀ from Namibia, Swakop River (22°41'S:14°35'E), on road to Goanikontes, 11.iv.1998, F.W. & S.K. Gess (AMGS).

Description:

Male.

Measurements (n=4): total body length 5.8 mm, head length 1.2 mm, head width 1.5 mm, lower interocular distance 0.8 mm, upper interocular distance 1.0 mm, interantennal distance 0.3 mm, antennocular distance 0.2 mm, length of clypeus 0.4 mm, length of eye 0.9 mm, length of facial fovea 0.3 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 0.8 mm, mesosoma length 1.8 mm, forewing length 3.7 mm, pterostigma length 0.5 mm, maximum width of pterostigma 0.2 mm, marginal cell length 0.9 mm, length of marginal cell beyond pterostigma 0.7 mm, length of freepart of marginal cell 0.6 mm, metatibia length 1.1 mm, metabasitarsus length 0.7 mm.

Vestiture: Clypeus, supraclypeal area, and lower paraocular area thickly covered in decumbent, white, bristly setae (integument obscured). Vertex with sparse, erect, longish, white setae. Gena densely covered in shortish, white setae. Mesoscutum fairly densely covered in short, whitish, erect setae (integument visible). Scutellum and metanotum similar to mesoscutum. Mesepisternum hairless dorsally, but thickly hairy below. Metepisternum largely nude. T2-T4 with bands of very short, bristly, white setae along graduli. Sterna very weakly hairy with feeble posterior hairbands S3-S5.

Integumental colour: Mostly black except for metasoma and legs. Scape, pedicel and flagellomeres orange-yellow, dorsal surface of flagellomeres dark brown. Mandible largely yellow except for distal black tip. Pronotal lobe dark brown with slight yellow tinge. Protibia and protarsi yellow. Profemur and protrochanter brown with orange tinge. Middle and hindlegs similar colour pattern to foreleg. T1 black, slightly orange posteriorly. T2 orange (fovea and area immediately adjacent black). T3 orange-brown. T4-T6 black. T7 orange.

Head (Prosoma): Clypeus densely punctate (interspace <0.5X puncture diameter), smooth and shiny interspaces, no medio-longitudinal clypeal sulcus, lower edge of clypeus emarginate. Supraclypeal area protuberant, anterior face of supraclypeal area densely punctate (interspace <0.5X puncture diameter). Paraocular area and frons densely punctate. Frontal line distally carinate. Facial fovea very narrow, slit-like. Vertex densely punctate, not carinulate. Gena densely punctate. Inner eye orbits diverging slightly dorsally, proportion of lower to upper interocular distance 0.8:1. Antenna fairly long, just reaching tegula, F1 weakly tapering to base, F1 approximately 1.4X length of F2.

Mesosoma: Pronotal lateral ridge weak. Mesoscutum densely punctate (interspace 0.5-1X puncture diameter), interspaces smooth and shiny, median line weakly impressed. Scutellum and metanotum similar sculpture to mesoscutum. Propodeum strongly angulate. Propodeal triangle with irregular network of carinae on basal area. Basal area of propodeal triangle quite long, 2X the length of metanotum. Mesepisternum fairly dense punctation, slightly roughened between punctures. Upper half of metepisternum with three transverse carinae in some specimens.

Metasoma: Tergal discs with dense punctation and smooth interspaces. T2 fovea elongate ovoid. Pygidial plate absent.

Terminalia: Gonobase large, inner margin of gonocoxite toothed posteriorly, gonoforceps curved inwards posteriorly, lightly hairy (Fig. 58). S6 weakly emarginate posteriorly, weak ridge adjacent to apodemes (Fig. 59). S7 posteriorly tapering to weakly emarginate point, outer margin of anterior arms with small protuberance (Fig. 60). S8 distal process short, fairly hairy, rounded (Fig. 61).

Legs: Metabasitibial plate with only posterior carina present, small distal tubercle sometimes present. Pretarsal claws deeply cleft.

Female.

Measurements (n=4): total body length 6.3 mm, head length 1.3 mm, head width 1.7 mm, lower interocular distance 1.0 mm, upper interocular distance 1.1 mm, interantennal distance 0.3 mm, antennocular distance 0.3 mm, length of clypeus 0.5 mm, length of eye 1.0 mm, facial fovea length 0.5 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 0.9 mm, mesosoma length 2.0 mm, forewing length 3.9 mm, pterostigma length 0.5 mm, maximum width of pterostigma 0.2 mm, marginal cell length 1.0 mm, length of marginal cell beyond pterostigma 0.8 mm, length of freepart of marginal cell 0.7 mm, metatibia length 1.2 mm, metabasitarsus length 0.7 mm.

Vestiture: Face largely naked, sparse white setae surrounding antennal sockets and feeble fringe to ventral margin of clypeus. Sparse, scattered, short white setae on mesoscutum,

thicker on scutellum and metanotum. Sides of mesosoma weakly hairy. T2-T4 with bands of short, white setae along graduli, expanding out onto disc on T4. Prepygidial fimbria thick, white, bristly setae. Metatibial scopa all-white setae. S2 plumose, white setae, remainder of sterna with sparse, white setae. Brush on anterior (outer) surface of probasitarsus with simple setae.

Integumental colour: Mainly black. Scape and pedicel brownish with slight orange tinge. Flagellomeres ventrally yellow, dorsally dark brown. Mandibles mostly yellow-orange. T1-T4 all orange. T5 mainly black. T6 orangish. Trochanter and femur on all legs brown with orange tinge. All tibia and tarsi orange-yellow.

Head (Prosoma): Clypeus with fairly dense punctation (interspace 1-1.5X puncture diameter), interspaces shiny and superficially smooth (but very faintly reticulate), no medio-longitudinal clypeal sulcus, lower edge of clypeus medially emarginate. Supraclypeal area strongly protuberant above adjacent antennal sockets. Anterior face of supraclypeal areas with rather sparse punctation, shiny with faint reticulation. Paraocular area, frons and vertex densely punctate (interspace 0.5-1X puncture diameter), interspaces smooth and shiny, vertex not carinulate. Frontal line distally carinate. Facial fovea slit-like. Eyes diverge very slightly dorsally, proportion of upper to lower interocular distance 1.0:1.1. Antenna just reaches tegula, F1 weakly tapering to base, F1 approximately 1.3X longer than F2.

Mesosoma: Lateral ridge of pronotum weak. Mesoscutum densely punctate (interspace 0.5-1X puncture diameter), anterior interspaces with faint reticulation, remainder smooth. Median line moderately impressed, notaulus very weak and barely evident. Scutellum sparsely punctate, interspaces shiny, superficially smooth with very faint reticulations. Propodeum strongly angulate. Basal area of propodeal triangle with short, longitudinal carinae, remainder of triangle roughened. Basal area of propodeal triangle approximately 1.7X longer than metanotum. Mesepisternum densely punctate with reticulate interspaces, pre-episternal groove pitted throughout.

Metasoma: Tergal discs with dense punctation and smooth interspaces. T2 fovea ovoid. Pygidial plate weakly tapering, rounded, dorsal surface smooth.

Terminalia: T7 sub-quadrate with moderately produced apodemal region, posterior edge curved and slightly produced ventro-posteriorly, spiracle placed far back but not opening onto posterior edge, lateral lamina fairly narrow (approximately 0.2X breadth of lamina spiracularis). Dorsal arm of furcula sub-equal in length to ventral arms. Condylar ridge area of T8 strongly curved. Apodeme of T8 extends beyond tergum.

Legs: Metabasitibial plate reduced to a ring of seven to nine irregularly-shaped tubercles. Pretarsal claws are simple.

Diagnosis: *S. pyretus* is a tiny black bee bee with an orange-red metasoma (Fig. 62). Other noteworthy features are the deep, slit-like facial foveae, largely yellow mandibles, slight yellow tinge to pronotal lobe, tuberculate metabasitibial plate in the ♀, and simple claws in the ♀. The ♂ *S. pyretus* keys close to ♂ *S. luridus* (due to the orangish scape), though, it is easily distinguished by the orangish metasoma (black in *S. luridus*), its smaller body length (approximately 8-9 mm in *S. luridus*), the different facial foveae (shallow and indistinct in *S. luridus*), the near-absent lateral pronotal ridge (sharp and well-defined in *S. luridus*) and the strongly divergent terminalia (see Eardley 1996: figs 78-80 for *S. luridus*). In general facies, the ♂ *S. pyretus* recalls *S. avius* or *S. calx*, but the mostly orange metasoma and orangish scape are distinctive. The ♀ *S. pyretus* is superficially similar to *S. avius*, but can be distinguished by its largely yellow mandibles (dark red-brown to black in *S. avius*), blunt lateral pronotal ridge (sharp-edged and well-defined in *S. avius*), and slit-like facial fovea with the bottom of the fovea not visible (*S. avius* facial foveae are also narrow but the bottom is clearly visible with reticulate sculpture).

Distribution: Namibian endemic, only known from the Gaub Pass and Swakop River area.

Biology: Specimens (both sexes) were caught visiting the yellow flowers of *Tetraena simplex* (L.) Beier & Thulin (Zygophyllaceae) in dry river-beds. The bees have been captured in March-April, suggestive of a late summer bee.

Scrapter sittybon sp. n.
Figs 63-66

Etymology: *sittybon* (Gr.) = small piece of parchment or skin. In reference to the unique S7 (Fig. 65).

Holotype ♂: SOUTH AFRICA: *Western Cape*: 40 km north-east of Vanrhynsdorp, Farm Kalkgat (31°07'04"S: 18°55'18"E), 140 m, 10.ix.2003, K. Timmermann (to be deposited in SANC). Paratype: 1 ♂collected 30 km north of Vanrhynsdorp in the Knersvlakte, 5-6.ix.2003 (MKPC).

Description:

Male.

Measurements ($n = 2$): head length 1.2 mm, head width 1.5 mm, lower interocular distance 0.8 mm, upper interocular distance 1 mm, interantennal distance 0.2 mm, antennocular distance 0.2 mm, length of clypeus 0.4 mm, length of eye 1 mm, width of eye (lateral view) 0.6 mm, width of gena (lateral view) 0.3 mm, length of facial fovea 0.2 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 0.8 mm, mesosoma length 1.7 mm, forewing length 3.2 mm, length of pterostigma 0.5 mm, maximum width of pterostigma 0.1 mm, length of marginal cell beyond pterostigma 0.6 mm, length of marginal cell 0.9 mm, length of free-part of marginal cell 0.6 mm.

Vestiture: Clypeus, anterior face of supraclypeal area and lower parts of paraocular area with thick, white, decumbent setae. Remainder of supraclypeal area, frons, vertex and upper parts of paraocular area with fairly dense, erect, whitish setae. Gena with short, whitish setae but thicker ventrally. Mesoscutum, scutellum and metanotum with short, plumose, gold-white setae. Sides of mesosoma with very sparse, whitish, plumose setae. T1 largely hairless except for very sparse, scattered, inconspicuous white setae. T2-T4 with distinctive bands of short, thick, white pubescence adjacent to graduli, remainder of discs hairless. T5-T6 sparse, plumose setae, setae stout on T6.

Integumental colour: Largely black. Antenna F1-F3 ventrally yellow-orange, dorsally blackish, F4-F11 all yellow-orange. Protibia, protarsus and extreme apical end of profemur all orange-yellow. Middle leg similar to foreleg. Extreme apical end of metafemur and proximal end of metatibia yellow-orange, metatarsus dark orange-brown.

Head (Prosoma): Clypeus shiny and smooth with heavy punctation (interspace <0.5X puncture diameter), no clypeal sulcus. Supraclypeal area, paraocular area and frons sculpture and punctation similar to clypeus. Ocellar triangle weakly raised in anterior profile. Facial fovea a sulcus. Frontal line weakly carinate. Gena much narrower than eye (0.5:1), with fairly dense punctation and reticulate sculpture. Inner eye orbits diverging

slightly dorsally, proportion of lower to upper interocular distance 0.8:1. Antenna long, reaching metanotum.

Mesosoma: Mesoscutum shiny and smooth with dense punctation (interspace 0.5-1X puncture diameter), median line and notaulus weakly impressed. Scutellum sculpture similar to mesoscutum but punctation less dense. Metanotum with roughened sculpture and heavy punctation. Mes- and metepisterna with weakly carinulate sculpture and fairly dense punctation. Propodeum angulate, sides of propodeum with clumped punctation and roughened sculpture, propodeal triangle with weak network of carinae throughout including longitudinal carinae on basal area, margins of triangle weakly pitted.

Metasoma: T1-T6 with reticulate sculpture on discs. T1-T4 with fairly dense punctation (interspace approximately 1X puncture diameter), T2-T4 punctation especially pronounced towards graduli. T5-T6 fewer, larger punctures which are not concentrated around the graduli. T2 fovea an elongate ovoid.

Terminalia: Genitalia fairly complex; gonobase very large, gonoforceps tapering to acute point posteriorly, not hairy, has several membraneous invaginations ventrally, penis valves curved inwards, short, spike-like projection on inner margin of valves (Fig. 63). S6 medio-posteriorly extended with rear margin slightly concave and hairy, anteriorly strongly concave (Fig. 64). S7 distinctive, concave posteriorly, two acute processes fringed by transparent, rounded appendages bearing hairy posterior margins (Fig. 65). S8 rounded anteriorly, fairly hairy on posterior process (Fig. 66).

Legs: Metabasitibial plate entire. Claws deeply cleft.

Female: Unknown.

Diagnosis: The S7 of *Scrapter sittybon* is distinctive in the genus, with characteristic posterolateral, transparent 'flaps'. Further general distinguishing features of *S. sittybon* include the lack of a medio-longitudinal clypeal sulcus, sulcoid facial fovea, entire metabasitibial plate, short pubescence on the anterior part of terga and bifid claws. *Scrapter sittybon* has similarities to the *S. nitidus* complex, but the lack of a clypeal sulcus and distinctive terminalia facilitate separation from that group.

Distribution: Only known from the Knersvlakte, near Vanrhynsdorp, Western Cape. See comments under *S. acanthophorus* regarding this region.

Biology: Type series collected in September. No data on pollen/nectar sources.

Scrapter viciniger sp. n.

Figs 67-70

Etymology: *vicinus* (L.) neighbouring, near, close to; *niger* (L) black. In allusion to its superficially similar appearance to *Scrapter niger*.

Holotype ♂: SOUTH AFRICA: *Northern Cape*: Nieuwoudtville Flower Reserve (31°21'56"S:19°08'52"E), 735m, 3.ix.2003, M. Kuhlmann (SANC). Paratypes: 2 ♂♂ with same data as holotype (MKPC) and 6 ♂♂ Farm Glen Lyon (31°23'50"S:19°08'26"E), Nieuwoudtville district between 11-12.ix.2003 (MKPC).

Description:

Male.

Measurements (n=4): total body length 8.9 mm, head length 1.8 mm, head width 2.2 mm, lower interocular distance 1.3 mm, upper interocular distance 1.6 mm, interantennal distance 0.4 mm, antennocular distance 0.4 mm, length of clypeus 0.6 mm, length of eye 1.3 mm, length of facial fovea 0.5 mm, maximum width of facial fovea 0.1 mm, mesoscutum length 1.2 mm, mesosoma length 2.6 mm, forewing length 6.1 mm, pterostigma length 0.9 mm, maximum width of pterostigma 0.2 mm, marginal cell length 1.5 mm, length of marginal cell beyond pterostigma 4.8 mm, length of free-part of marginal cell 1.0 mm, metatibia length 1.7 mm, metabasitarsus length 1.1 mm.

Vestiture: Clypeus and lower paraocular area with thick, appressed, minutely plumose, white setae (underlying integument completely obscured). Supraclypeal area, upper paraocular area, frons and vertex sparse, erect, plumose greyish setae. Gena fairly thick, white, plumose setae. Mesoscutum moderate cover of long, erect, weakly plumose, greyish setae (underlying integument easily visible). Scutellum and metanotum similar to mesoscutum but setae thickers and base of setae dark, imparting brownish impression to vestiture. Plumose, greyish setae, setae thicker on propodeum with dark bases creating brownish impression. T1 sparse setae anteriorly. T2-T4 fairly dense, sub-erect, minutely

plumose whitish setae, thicker anteriorly (underlying integument can easily be seen). No tergal bands. S2-S5 incurved, sparse, minutely plumose setae, no distinct bands on sterna.

Integumental colour: Mainly black. Slight orange tinge to ventral surface of antenna. Metasoma with orange-brown tinge. No yellow on legs or antenna.

Head (Prosoma): Clypeus densely punctate (interspaces 0.5X puncture diameter), interspaces smooth, no medio-longitudinal clypeal sulcus. Supraclypeal area weakly elevated, anterior face of supraclypeal area largely punctureless, smooth and shiny. Lower paraocular area densely punctate (interspaces 0.5X puncture diameter). Frons, upper paraocular area and vertex strongly carinulate. Facial fovea narrow, shallow ovoid with roughened sculpture inside. Gena with fairly dense punctation, near-carinulate. Antenna long, when extended backwards reaches propodeum.

Mesosoma: Pronotum lacking lateral ridge. Mesoscutum densely punctate (interspaces 0.5X puncture diameter), anterior third, lateral edges and posterior edge of mesoscutum roughened, remainder smooth. Scutellum and metanotum similar to mesoscutum but roughened throughout. Pre-episternum and mesepisternum with moderate punctation, coarsely roughened and longitudinally carinulate. Hypoepimeral area uniformly roughened with no carinae. Metepisternum and sides of propodeum with sparse punctation and uniform coriaceous sculpture (not carinulate). Propodeum near-declivitous. Propodeal triangle with weak, short carinae on narrow basal area, remainder of triangle uniformly coriaceous roughening. Basal area of propodeal triangle approximately same length as metanotum.

Metasoma: T1 anteriorly minutely roughened and densely punctate, posterior third shiny and smooth. T2-T4 very fine sculpture and densely punctate. T7 with weak pygidial plate. T2 fovea short, weakly-defined ovoid.

Legs: Metabasitibial plate entire. Pretarsal claws deeply cleft.

Terminalia: Gonobase large, inner margin of gonocoxite conspicuously toothed, gonoforceps curved inwards posteriorly, penis valves narrow (Fig. 67). S6 rounded posteriorly with hairy tuft on apex, meso-laterally are two separate sets of curved carinae

(Fig. 68). S7 concave posteriorly with tufts of setae postero-laterally (Fig. 69). S8 posterior process rounded and hairy (Fig. 70).

Female. Unknown.

Diagnosis: *Scrapter viciniger* is very similar in appearance to *S. niger*. To distinguish this species from *S. niger* the terminalia need to be extracted. The toothed inner margin of the gonocoxite of *S. viciniger* is characteristic (Fig. 67). General characteristics of *S. viciniger* include a carinulate vertex and frons, largely smooth mesoscutum, entire metabasitibial plate, propodeal triangle with uniform sculpture, and dark (as opposed to yellowish) tarsi; these traits are similar to *S. niger*.

Distribution: Only known from the Nieuwoudtville district, Northern Cape (Succulent Karoo biome).

Biology: Specimens have been caught on *Oxalis* sp. (Oxalidaceae) and *Eriocephalus ericoides* (L.f.) Druce (Asteraceae). The limited data suggests the flight period is during the austral spring (September).

3.4. Previously undescribed females

Scrapter albifumus Eardley, 1996

Scrapter albifumus Eardley, 1996: 74, figs 70-72, 81. (Type locality: Cornell's Kop, Richtersveld, Northern Cape)

Description:

Female.

Material examined: 4 ♀♀ SOUTH AFRICA: *Northern Cape*: Richtersveld National Park (28°18'S: 16°58'E), 12-14.ix.2001, C. Eardley (SANC); 8 ♀♀ on road to Richtersveld National Park between Annis and Dabie River (28°20'S: 16°55'E), 19.ix.1997, F.W. and S.K. Gess (AMGS); 7 ♀♀ Richtersveld National Park, 1.5 km from Helskloof (28°18'S: 16°57'E), 19.ix.1997, F.W. and S.K. Gess (AMGS).

Measurements (n = 3): head length 1.4 mm, head width 1.7 mm, lower interocular distance 1.1 mm, upper interocular distance 1.1 mm, interantennal distance 0.3 mm, antennocular distance 0.3 mm, length of clypeus 0.4 mm, length of eye 1.1 mm, width of eye (lateral view) 0.5 mm, width of gena (lateral view) 0.3 mm, length of facial fovea 0.4 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 1 mm, mesosoma length 2 mm, forewing length 4.1 mm, length of pterostigma 0.6 mm, width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 1 mm, length of marginal cell 1.1 mm, length of free-part of marginal cell 0.7 mm.

Vestiture: Very hairy bee, setae generally short, bristly and compact. Clypeus, supraclypeal area and lower paraocular area with sparse, white, decumbent, bristly setae. Upper paraocular area and frons with fairly thick, erect, white setae. Vertex similar to frons but setae sparser. Scape with a few, very short, white setae. Gena with thick, white, bristly setae. Mesoscutum with short, yellowish, bristly, moderately dense setae. Scutellum and metanotum similar to mesoscutum but with longer, denser, more orangish setae. Mes- and metepsiterna with long, white, fairly dense, bristly setae. Propodeum with thick, largely plumose, white setae. T1-T4 with conspicuous, posterior, white, hair-bands along marginal zones. T1 anteriorly with fairly dense, white vestiture (but integument easily visible). Sides of discs on T1-T4 with sub-erect, bristly, white setae. T5 prepygidial fimbria composed of thick, white and bristly setae. S1-S2 bearing palmate-haired scopa, remaining sterna weakly hairy. Anterior probasitarsal brush with simple setae. Metatibial scopa composed of all white, plumose, setae except posteriorly where long, white, simple keirotrichia present.

Integumental colour: Mainly black. Undersides of F1-F8 and all of F9-F10 orange. Apical end of profemur, protibia and protarsus orange.

Head (Prosoma): Clypeus and supraclypeal area with finely reticulate sculpture and moderately dense punctation (interspace 1X puncture diameter). Paraocular area and frons sculpture similar to clypeus but punctation denser. Facial fovea a sulcus. Frontal line extremely weak. Ocellar triangle very weakly raised in anterior profile. Gena narrower than eye (0.6:1), with dense punctation (interspace 0.5-1X puncture diameter). Inner eye orbits straight, proportion of lower to upper interocular distance equal. Antenna shortish, reaching tegula.

Mesosoma: Mesoscutum with shiny, reticulate sculpture and dense punctation (interspace 0.5-1X puncture diameter), median line and notaulus very weak. Scutellum and metanotum sculpture similar to mesoscutum but punctation reduced on anterior part of scutellum. Mesepisternum with coarsely reticulate sculpture and fairly dense punctation, episternal

groove arced forward, pitted throughout. Propodeum strongly angulate, with coarse reticulation and fairly dense punctation, propodeal triangle with uniform, reticulate sculpture and no carinae.

Metasoma: Tergal discs with fine, reticulate sculpture and scattered punctation, punctures denser and larger on T5. T2 fovea ovoid.

Legs: Metabasitibial plate entire, rather round, extremely hairy. Claws toothed.

Remarks: These are the first females of *S. albifumus* found, and all were collected in the Richtersveld. Most of the ♂ *S. albifumus* specimens Eardley (1996) listed were also collected in the Richtersveld. The distinctive features of this region are discussed under *S. chrysomastes*. Eardley (1996: 74) noted that the males 'usually die with the metasoma curved under the body'. In the female specimens collected in September 2001, this is also the case, and gives the bees a characteristic posture on the pin (Fig. 71). However, the samples collected by Drs F.W. and S.K. Gess are not curled on their pins and have the setae matted down and distorted (from excess ethyl acetate in the killing bottle). The species has been recorded foraging on *Tetraena prismatocarpa* E. Mey. ex Sond. (Zygophyllaceae) by F.W. and S.K. Gess.

Scrapter amplispinatus Eardley, 1996

Scrapter amplispinatus Eardley, 1996: 80-81, figs 81, 88-90. (Type locality: Hartebeesfontein Farm, Middelpos, Northern Cape)

Description:

Female.

Material examined: 1 ♀ SOUTH AFRICA: *Northern Cape*: Elandsfontein (31°46'S: 20°03'E), 16.ix.1999, V. Whitehead (SAMC).

Measurements (n = 1): head length 2.6 mm, head width 3 mm, lower interocular distance 2 mm, upper interocular distance 2.1 mm, interantennal distance 0.4 mm, antennocular distance 0.6 mm, length of clypeus 0.8 mm, length of eye 1.8 mm, width of eye (lateral view) 1.1 mm, width of gena (lateral view) 0.5 mm, length of facial fovea 0.7 mm, maximum width of facial fovea 0.2 mm, mesoscutum length 1.9 mm, mesosoma length 3.5 mm, forewing length 8.1 mm, length of pterostigma 1.1 mm, maximum width of pterostigma 0.3 mm, length of marginal cell beyond pterostigma 1.7 mm, length of marginal cell 2.1 mm, length of free-part of marginal cell 1.3 mm.

Vestiture: Clypeus, supraclypeal area, paraocular area and frons with sparse, black, weakly plumose, sub-erect setae. Vertex similar but setae erect. Gena adjacent to eye with sparse, black setae, gena towards occiput with thick, white, plumose setae. Mesoscutum covered in short, fairly dense (integument easily visible), erect, yellowish, plumose setae, some taller black setae intermixed. Scutellum and metanotum similar to mesoscutum but with thicker, longer, yellower setae. Mes- and metepisterna with long, fairly dense, white setae. Propodeum with fairly dense, strongly plumose setae. T1-T4 with distinct posterior, white hair-bands along marginal zones, remainder of discs with sparse, short, whitish setae, particularly laterally. T5 prepygidial fimbria composed of thick, black, mostly plumose, decumbent setae. S1 and S2 centrally with fairly thick, strongly plumose scopa, remaining sterna with moderate vestiture. Anterior probasitarsal brush setae simple. Metatibial scopa anteriorly bearing white, plumose setae, dorsally with ridge of dark, plumose setae, posteriorly thick, white, simple keirotrichia.

Integumental colour: Largely black. Antenna ventrally orange. Hindlegs with orangish wash.

Head (Prosoma): Broad. Clypeus with finely reticulate sculpture and dense punctation (interspace 0.5X puncture diameter), clypeal sulcus present. Supraclypeal area, paraocular area, and frons sculpture and punctation similar to clypeus. Frontal line largely carinate. Facial fovea broad, shallow, shiny and conspicuous. Vertex rounded in anterior profile. Gena much narrower than eye (0.5:1), with dense punctation, almost carinulate. Inner eye orbits straight, proportion of lower to upper interocular distance equal. F1 slightly elongate. Antenna quite long, reaching scutellum.

Mesosoma: Mesoscutum with very dense, uniform punctation (interspace <0.5X puncture diameter), narrow interspaces weakly reticulate. Scutellum and metanotum sculpture and punctation similar to mesoscutum. Mesepisternum with roughened, near-carinulate sculpture and dense punctation (interspace 1X puncture diameter), episternal groove pitted throughout, although weakly above. Propodeum declivitous, fairly dense punctation and coarse, reticulate sculpture, propodeal triangle greatly reduced forming three acute points, uniform reticulate sculpture.

Metasoma: T1-T4 discs with dull, roughened, dense reticulate sculpture and micropunctation. T5 similar but with larger punctures. T2 fovea very broad and rounded.

Legs: Metabasitibial plate composed of two carinae (anterior and posterior), posterior carina becomes tuberculate apically (three separate tubercles). Claws simple.

Remarks: *Scrapter amplispinatus* was described from Middelpos in the Roggeveld Moutains of the Northern Cape. The present female specimen (Fig. 72) was also collected from the Roggeveld Mountains together with three males. Two of the males and the female were collected on flowers of *Polycarena aurea* Benth. (Scrophulariaceae). The remaining male was collected on a *Selago* species (Scrophulariaceae). The Roggeveld Mountains fall within the Succulent Karoo biome, and the area forms part of the 'Hantam-Roggeveld Centre' of plant endemism (Van Wyk & Smith 2001: 72-81). The region is characterised by low, mainly winter rainfall (usually less than 300 mm) and exceedingly cold winters (night temperatures usually fall well below 0°C during winter). The Roggeveld region is noted for its exceptionally rich asilid fauna (Londt 1994: 119-120), and it is possible many insects occurring in the area will be found to be endemics. *Scrapter amplispinatus* is evidently such an endemic. The male of the species has a greatly swollen anterior (outer) metatibial spur (hence the specific epithet), the female has an unmodified anterior metatibial spur.

3.5. A significant range extension of the genus

Scrapter nitidus (Friese, 1909)

Polyglossa nitida Friese, 1909: 124 (Type locality: Steinkopf, Namaqualand, Northern Cape)
Polyglossa (Strandiella) nitida Friese: Friese 1925: 514
Scrapter nitidus (Friese): Cockerell 1936: 481
Scrapter nitidus (Friese): Eardley 1996: 43-45.

Material examined: 1 ♀ KENYA: Rukinga Ranch, Pikapika Lodge (03°55.1S ; 39°24.5E), 25.vi.2003, W. Kinuthia, D. Martins, C. Eardley and B. Gemmill (SANC).

Remarks: Basic measurements of this specimen are - head length 1.7 mm, head width 2.1 mm and mesoscutum length 1.3 mm. This single specimen keys out to *S. nitidus* in Eardley's (1996) key and agrees excellently with Eardley's redescription of the species. I compared the Kenyan specimen against *S. nitidus* specimens from Villiersdorp and Ceres (Western Cape, South Africa) and, despite careful examination, could find no meaningful differences between them. Identifying features of the Kenyan specimen include the presence of a clypeal sulcus, slit-like facial fovea, 'concertina-like' propodeal triangle sculpture (see Eardley 1996, fig. 2), entire metabasitibial plate, dense mesoscutal punctation, black prepygidial fimbria and raised ocellar triangle (all characteristic features of *S. nitidus*). The specimen has an all-black metasoma, simple claws and antennae that extend to the tegulae.

Scrapter nitidus was previously believed to extend from the KwaZulu-Natal Drakensberg foothills southwards to the Western Cape and then northward to Namaqualand, Northern Cape. Most specimens have been collected in the Fynbos and Succulent Karoo biomes (Eardley 1996). Rukinga Ranch is part of Tsavo Game Reserve, southern Kenya, and is an enormous and unexpected range extension of *S. nitidus* and the genus itself. The most northerly record to date of *Scrapter* was of *S. absonus* Eardley from Victoria Falls, Zimbabwe. The collection site at Rukinga Ranch is a dry, hot, low-lying area dominated by *Commiphora* woodland (C.D. Eardley pers. comm.). Very few *Scrapter* species have been recorded from savanna. The remarkable discovery of *Scrapter* in East Africa suggests there are probably other *Scrapter* species distributed through Mozambique, Tanzania and Kenya.

Table 1. Flower visiting records of *Scrapter*. Sources: 1=Eardley (1996), 2=Gess & Gess (2003), 3=Davies, G. pers. obs., 4=South African Museum label data, 5=Kuhlmann, M. pers. obs.

Family	Genera	*Scrapter* species
Proteaceae	*Leucadendron* sp. and *Paranomus bracteolaris* Salisb. ex Knight	*S. erubescens* (Friese)[1]
"	*Leucadendron* sp.	*S. fuliginatus* Eardley[1]
Aizoaceae	*Conocosia* sp. and *Herrea* sp.	*S. bicolor* Lep. & Serv.[1,3]
"	*Ruschia* sp.	*S. chloris* Eardley[1]
"	*Herrea* sp.	*S. algoensis* (Friese)[2]
"	*Herrea* sp.	*S. capensis* (Friese)[2]
Scrophulariaceae	*Diascia* sp.	*S. nitidus* (Friese)[4]
"	*Diascia* sp.	*S. capensis* (Friese)[1]
"	*Hemimeris* sp.	*S. chloris* Eardley [1]
"	*Polycarena* sp.	*S. algoensis* (Friese)[4]
"	*Polycarena* sp. and *Selago* sp.	*S. amplispinatus* Eardley[1]
"	*Polycarena* sp.	*S. erubescens* (Friese)[1]
Asteraceae	*Chrysocoma strigosa* E. Bayer, *Dimorphotheca sinuata* DC., *Euryops thunbergii* B. Nord., *Helichrysum rugulosum* Less., *Othonna* sp., *Senecio cardaminifolius* DC. and sp.	*S. nitidus* (Friese)[1,2]
"	*Athanasia trifurcata* (L.), *Helichrysum* sp., *Lasiospermum bipinnatum* (Thunb.) Druce, *Othonna cylindrinca* (Lam.) DC., *Pentzia suffruticosa* (L.) Hutch. ex Merxm., *Senecio rosmarinifolius* L.f.	*S. ruficornis* (Cockerell) [1,2]
"	*Conyza podocephala* DC.	*S. basutorum* (Cockerell)[4]
"	*Helichrysum* sp.	*S. pallidipennis* (Cockerell)[4]
"	*Helichrysum* sp. and *Pentzia suffruticosa* (L.) Hutch. ex Merxm.	*S. flavostictus* Cockerell[1,2]
"	*Arctotheca calendula* (L.), *Arctotis* sp., *Dimorphotheca* sp., *Gazania* sp., *Osteospermum* sp.	*S. heterodoxus* (Cockerell)[1,2]
"	*Cotula* sp.	*S. catoxys* Davies[2]
"	*Arctotheca calendula* (L.), *Gymnodiscus linearifolia* DC., *Helichrysum* sp., *Senecio* sp.	*S. niger* Lep. & Serv. [1,2]
"	*Senecio* sp.	*S. leonis* Cockerell[1]
"	*Gymnodiscus linearifolia* Thunb.	*S. algoensis* (Friese)[2]
"	*Pentzia incana* (Thunb.) Kuntze	*S. capensis* (Friese)[2]
Zygophyllaceae	*Roepera foetida* (= *Zygophyllum meyeri* Sond.) and *Tetraena prismatocarpa* (= *Zygophyllum prismatocarpum* E. Mey. ex Sond.)*	*S. albifumus* Eardley[2]
"	*Roepera foetida* (= *Zygophyllum meyeri* Sond.)*	*S. chrysomastes* Davies[2]
"	*Roepera foetida* (= *Zygophyllum meyeri* Sond.) and *Tetraena prismatocarpa* (= *Zygophyllum prismatocarpum* E. Mey. ex Sond.)*	*S. tomentum* Eardley[2]
"	*Tetraena simplex* (= *Zygophyllum simplex* L.)*	*S. pyretus* Davies[2]
Oxalidaceae	*Oxalis* sp.	*S. oxyaspis* Davies[5]
"	*Oxalis* sp.	*S. carysomus* Davies[5]
"	*Oxalis* sp.	*S. eremanthedon* Davies[5]
Brassicaeae	*Heliophila* sp.	*S. albitarsis* (Friese)[5]
"	*Heliophila* sp.	*S. amplitarsus* (Friese)[2]
"	*Brassica* sp.	*S. leonis* Cockerell[1]
Neuradaceae	*Grielum* sp.	*S. avius* Eardley[4]
"	*Grielum humifusum* Thunb., *G. sinuatum* Licht. ex Burch., *G. grandiflorum* (L.) Druce	*S. chloris* Eardley[1,3]
"	*Grielum sinuatum* Licht. ex Burch. and sp.	*S. luridus* Eardley[1]
"	*Grielum* sp.	*S. whiteheadi* Eardley[1]

*South African *Zygophyllum* transferred to *Roepera* and *Tetraena* in Beier *et al.* (2003)

3.6. Status of five Cockerell taxa

Scrapter niger Lepeletier de Saint-Fargeau & Audinet-Serville, 1828

Scrapter niger Lepeletier de Saint-Fargeau & Audinet-Serville, 1828: 403 (Type locality: 'Cafrarie')

Scrapter subincertus Cockerell, 1944*a*: 405 **syn. n.** (Type locality: Rapenburg, Cape Flats, Cape Town, Western Cape)

Scrapter brunneipennis Cockerell, 1944*a*: 406 **syn. n.** (Type locality: Mossel Bay, Western Cape)

Scrapter subincertus (Fig. 73) was briefly described from females collected at Rapenburg, Western Cape in early October by Rowland Turner. Cockerell (1944*a*) wondered 'whether this could be the female of *S. niger*, but what I have identified as probably *S. niger*, from Natal, is certainly different'. Cockerell's remarks are rejected because *S. niger* does not occur in KwaZulu-Natal (Eardley 1996: fig. 62), and a *S. subincertus* syntype agrees excellently with material from Dassiefontein, Kamieskroon district, Northern Cape identified as *S. niger* by C.D. Eardley. Identifying features include the presence of a clypeal tubercle, nascent clypeal sulcus, sharply-defined ovoid facial foveae with finely reticulate sculpture, weakly carinulate vertex and frons, dense mesoscutum punctation (interspace 0.5-1X puncture diameter) with smooth interspaces and scattered micropunctures, weakly angulate propodeum (propodeal triangle basal area subequal in length to metanotum) with feeble carinae on propodeal triangle basal area, tuberculate metabasitibial plate, simple claws and brush on anterior (outer) surface of probasitarsus with both simple and branched setae.

The status of the material identified as probable *S. niger* from KwaZulu-Natal by Cockerell is uncertain; it is possibly in The Natural History Museum, London. Cockerell (1935: 239) also mentioned male bees from KwaZulu-Natal Drakensberg that he tentatively identified as male *S. niger*.

Cockerell (1944*a*) described *S. brunneipennis* (Fig. 74) from male specimens obtained at Mossel Bay, Western Cape by Rowland Turner in August 1932. I have examined a syntype and the genitalia agree closely with that of *S. niger* illustrated by Eardley (1996: fig. 57). Other features include: carinulate frons and vertex, no medio-longitudinal clypeal sulcus, finely reticulate mesoscutum surface with heavy punctation, metabasitibial plate not entire (jagged posterior carina and weak anterior carina), pygidial plate present, and all tarsi and protibia yellowish. The male holotype of *S. niger* in the Paris Museum is apparently now untraceable (C. Villemant *in. litt.*). *S. brunneipennis* is here synonymised with *S. niger*.

Scrapter leonis Cockerell, 1934

Scrapter leonis Cockerell, 1934: 452 (type locality: Lion's Head, Cape Town, Western Cape)
Scrapter merescens Cockerell, 1944*a*: 405 **syn. n.** (type locality: Worcester, Western Cape)

Scrapter merescens (Fig. 75) was perfunctorily described on the basis of seven females from Worcester in the Western Cape collected by Rowland Turner during August to September 1928 (Cockerell 1944*a*). I have examined a female syntype and found that it is attributable to *S. leonis*. Cockerell (1944*a*: 406) compared *S. merescens* to *S. leonis*, but distinguished it on the basis of 'duskier wings and the absence of red hair on the scutellum, as well as the broader head'. These seem trifling differences and *S. merescens* is here synonmyised with *S. leonis*.

Cockerell (1944*a*: 406) also mentioned a male specimen from Worcester that he thought may belong to *S. merescens*. I have examined this specimen. The handwritten label by Cockerell reads '*Scrapter merescens*, probable M, C[oc]k[ere]ll'. Cockerell did not describe this male in his 1944 paper, and clearly did not intend it to form any part of the syntype material. My examination of the specimen shows that it is unequivocally a specimen of *S. capensis* (Friese) as shown by the lack of a medio-longitudinal clypeal sulcus, carinulate frons and vertex, narrow, shallow facial fovea, leathery mesoscutal sculpture, almost entire metabasitibial plate (slight gap distally), short, plumose tomentum on S2 and S3 and truncate S8 and distinctly bifid claws. As the male specimen does not form part of the original syntype series, it has no nomenclatural standing and has merely been labelled as a specimen of *S. capensis*.

Scrapter algoensis (Friese, 1925)

Polyglossa (*Strandiella*) *algoensis* Friese, 1925: 519 (Type locality: Algoa Bay, Western Cape)
Polyglossa (*Polyglossa*) *rufofasciata* Friese, 1925: 518 (Type locality: Port Nolloth, Northern Cape)
Scrapter algoensis (Friese): Eardley 1996: 72
Scrapter sinophilus Cockerell 1944*a*: 406 **syn. n.** (Type locality: Mossel Bay, Western Cape)

Cockerell (1944*a*) described *S. sinophilus* (Fig. 76) from 12 males and 4 females collected by Rowland Turner at Mossel Bay. I have examined four male syntypes which agree well with material identified as *S. algoensis* by C.D. Eardley, in particular the genitalia accord closely (see Eardley 1996: figs 67-69), and *S. sinophilus* is here synonymised with that species.. Other relevant features of the males include: no medio-longitudinal clypeal

sulcus, antennae long reaching propodeum if extended backwards, vertex and frons not carinulate, mesoscutum with dense punctation and finely reticulate interspaces, propodeum slightly angulate, propodeal triangle with uniform, leathery sculpture throughout, and metabasitibial plate not entire (posterior carina plus a few small tubercles delimiting margin of plate).

Ctenoplectrina ugandica (Cockerell, 1944) **comb. n.**

Scrapter ugandica Cockerell 1944*b*: 805 (Type locality: Madi, Uganda)

Cockerell (1944*b*) described *S. ugandica* on the basis of a single female (Figs 77, 78) collected in May 1927, and he expressed surprise to 'find this South African genus so far north as Uganda'. Examination of the holotype female indicates that *S. ugandica* is not a colletid, let alone a *Scrapter* species.

Dissection of the mouthparts revealed it to have a fairly long, acute glossa. Other features arguing against it being a colletid include the lack of a pre-episternal groove (ignoring Diphaglossini and *Hesperocolletes* Michener), lack of arolia and absence of facial foveae. The labial palp segments are sub-equal in length, which suggested some sort of 'short-tongued' bee (possibly in Andrenidae, Halictidae or Melittidae). The general facies of the bee, however, was not similar to these 'short-tongued' taxa, and a stipital concavity with a weak comb was detected during the dissection of the mouthparts. There was also no trace of a galeal comb. These are features of a 'long-tongued' bee. Keying the specimen brought it out at Ctenoplectrini (Apidae), and this identification was confirmed by the marginal cell being sharply bent away from the costal margin (Fig. 79), a feature Michener & Greenberg (1980: 191) identify as 'a unique synapomorphy of the Ctenoplectridae'. Further confirmation was provided by the oil-collecting setae on S3-S5 (Fig. 80). Other characters of this bee include the short, compressed F1-F3 (contrasting with other flagellomeres), short, blunt mandibles with weak sculpture, lack of a ventral premental fovea, two submarginal cells, declivitous propodeum, lack of T2 fovea, weak, thin pygidial plate and deeply cleft claws.

There are only two ctenoplectrinid genera, *Ctenoplectra* Kirby and the parasitic *Ctenoplectrina* Cockerell. *Scrapter ugandica* is ascribed to the latter because it lacks a metabasitibial plate and has reduced oil-collecting tufts on the sterna. Michener (2000: 678) admitted one species in *Ctenoplectrina*, but noted 'the diversity among three specimens suggests two species'. Consequently I have moved the species to

Ctenoplectrina, but left in abeyance its relationship to the only other formally described species, *C. politula* Cockerell.

CHAPTER 4

ASPECTS OF THE MORPHOLOGY OF *SCRAPTER*

Morphological features of *Scrapter* that are poorly known or show pronounced variation are discussed in this chapter. Furthermore, aspects of morphology that have featured prominently in colletid (and bee) literature are also examined. Brief comparative notes describing the structure in other colletid bees are appended to the end of each subsection (where relevant).

Labrum

Due to time constraints and the less abundant material of male *Scrapter* specimens, I investigated the labrum in females only. The labrum is divided into two sections, an elevated, smooth, transverse, hairless *basal area* and a lower, hirsute *distal process* (Fig. 81). The sclerite is broader than long in all *Scrapter* species examined. The breadth:length ratio, however, varies greatly from 1.1:1 (i.e. sub-equal, e.g. *S. amplispinatus* Fig. 82) to 3:1 (e.g. *S. bicolor* Fig. 83).

There is substantial variation on the basic conformation of the labrum. The type species, *Scrapter bicolor*, is unique in the genus in having the *distal process* greatly reduced (Fig. 83). In some (e.g. *S. ruficornis* Fig. 84, *S. flavipes* (Friese) Fig. 86) the apex of the distal process is constricted forming a small, narrow point ('snout'); in others the distal process is broadly round to sub-truncate (e.g. *S. algoensis* (Friese) Fig. 85). The structure of the basal area also varies. It may be greatly reduced (e.g. *S. flavipes* Fig. 86). In some the basal area is bituberculate (e.g. *S. albifumus* Fig. 87). The anterior margin of the basal area is usually slightly pointed, sometimes sharply so (e.g. *S. chloris* Fig. 88). A medial depression is often in evidence on the basal area (e.g. Fig 83). The setae on the distal process are always simple and tapering. The deployment of setae on the distal process varies; they may be concentrated around the distal margins (e.g. *S. flavipes* Fig. 86), generally distributed across the distal process (e.g. *S. amplispinatus* Fig. 82) or concentrated in a longitudinal, medial band (e.g. *S. chloris* Fig. 88).

There is no thorough review of bee labra, and the treatment and illustration of colletid labra in the literature is patchy. In South American *Leioproctus*, the distal area is frequently reduced (like *S. bicolor*) with the labrum being >3X as wide as long (e.g. Michener 1989: fig 2e), although some species have labra reminiscent of many *Scrapter* species (e.g. Michener 1989: fig 6i).

Glossa and paraglossa

The glossa in *Scrapter* conforms to the basic colletid type (McGinley 1980), which has to perform (in the female) two principal functions: (a) the loading and conveyance of nectar/pollen into the food canal, and (b) the application of the transparent membranous lining to the brood cells. In *Scrapter* the glossa is weakly bilobed (i.e. medially emarginate on the apical margin) to sub-truncate, approximately twice as wide as long and considerably shorter than the prementum (prementum 2–4.5 X as long as the glossa).

The glossa is divided into distinct sections (Fig. 89). Distally the *glossal brush* is borne on the *glossal lobes*, an extension of the *disannulate surface* (the ventral surface of the glossa). The *glossal brush* (Fig. 90) is dense with simple to branched setae (the nature of the setae is not easy to determine). The glossal lobes are narrow and separated from the remainder of the glossa by the *pre-apical fringe*, a distinct line of strongly compressed setae. The *annulate surface* of the glossa takes up approximately ¾ of the glossa and consists of the *basiglossal sclerite* (which is undivided in scrapterines examined, Fig. 91), *pre-annular area* and *annular area*. The annular area (Fig. 92) is thickly covered in *glossal setae*, which are deployed in approximately 10-20 tightly-packed, transverse rows or annuli. The setae are sub-erect, spatulate, and, as described by Laroca *et al.* (1989) for *Niltonia* Moure (Colletinae *sensu* Michener), the lateral margins of these setae are infolded and nearly touching, imparting a tubular nature to the basal part of the setae. The glossa in *Scrapter* lacks clearly differentiated *basal* and *apical annular areas*, as also detected by McGinley (1980: fig. 9). The pre-annular area (Fig. 91, 93) is comprised of approximately six rows of rather elongate, appressed, blunt-tipped setae. At the pre-annular/annular area junction, the setae are strongly flattened and compressed together. The *spiculate zone* of the pre-annular area is very restricted in *Scrapter*. I could not detect the *basiglossal sensilla* in my dissections, although McGinley (1980: fig. 9) illustrated them for '*Parapolyglossa paradoxa*' (= *Scrapter heterodoxus*).

Overlapping and adjoining the basal and lateral portions of the glossa are the *paraglossae*. The *suspensorium of the paraglossa* is a large sclerite with a conspicuous row of approximately ten setae along the apical margin (Fig. 89). The paraglossa is elongate with a spatulate terminus and is hairy on the inner surface (Figs 89, 94).

The glossae of colletids have been studied by McGinley (1980), Michener & Brooks (1984) and Michener (1992), amongst others. McGinley (1980: 546) reported that glossal lobes are absent in the Euryglossinae. I examined one euryglossine exemplar (Fig. 95), and also found the glossal lobes greatly reduced (whether completely absent is more equivocal). If the absence or reduction of glossal lobes is true throughout the euryglossines, it may represent an apomorphy because clearly discernable glossal lobes are present in other colletids. Michener (1992: fig. 9) presented a hand-derived dendrogram (which he called a 'summary of glossal characters') of colletid relationships derived from nine binary glossal characters. *Scrapter* grouped with the 'other Colletidae' clade (composition of this clade not fully explained, but definitely including traditional Colletinae) that represented the sister-group to the Euryglossinae + Hylaeinae clade. The Euryglossinae + Hylaeinae clade was supported by a single character (annuli sharply segregated into basal and apical annular areas).

The morphology of the bee glossa and mouthparts, in general, has been extensively studied by melittologists. Indeed, proboscidial characters form a bulwark of many bee classifications and keys. By contrast, hymenopterists studying crabronid wasps have devoted relatively little attention to mouthparts (e.g. the nugatory coverage in Bohart & Menke 1976), and Ulrich's (1924) pioneering study has no modern equivalent. This pronounced research asymmetry in the two sister-groups is worrying. As the phylogeny of bees is so sensitive to interpretations of glossal morphology (e.g. Series 1 vs Series 2 analyses in Alexander & Michener 1995), an exhaustive modern survey of crabronid wasp mouthparts is now an urgent requirement.

Prementum

Both sexes of all *Scrapter* species examined have a fovea on the ventral (posterior) surface of the prementum (Fig. 96). The fovea is ovoid in shape and opens anteriorly onto the sublingual surface. Posteriorly a ridge extends into the proximal third of the fovea. The fovea is densely packed with small spicules (Fig. 97). Although the length and breadth of the fovea varies in *Scrapter*, the structure of the fovea appears conservative in the group. The function of the fovea is unknown. A foveate prementum is absent in Colletinae (*sensu*

Michener), but is found in hylaeines and xeromelissines (e.g. Michener 2000: fig. 38-19a), while euryglossines have a trend towards a spiculate fovea on the distal area of the prementum.

Postmentum (= *lorum and mentum* auct.)

The terminology and homology of the proximal sclerites of the bee labium have been the cause of substantial debate (reviewed in Plant & Paulus 1987). Essentially, the labium in bees comprises two sclerites – the distal, ligula-bearing sclerite (= *prementum*) and a proximal sclerite occupying the space between the inner apices of the cardines and the base of the stipites (= *postmentum*) (Fig. 98). These sclerites are separated by a tough membrane, the *interscleritic labial membrane* (= 'intersclerite membrane with mesocuticular outline' of Plant & Paulus (1987)). The proximal sclerite (= *postmentum*) may be subdivided in some bees into two different sclerites, which Winston (1979: 641) and Michener (1984, 2000) have termed the *lorum* and *mentum*. Plant & Paulus (1987) restricted use of the terms lorum and mentum to the Apinae (*sensu* Michener 2000), and argued that distinct lora and menta were absent in other bees. I consider the arguments of Plant & Paulus (1987) correct.

In *Scrapter*, two different basal-sclerite arrangements are observed: (1) a flat plate between the distal ends of the cardines linked by the tough interscleritic labial membrane to the basal apodeme of the prementum, with the interscleritic membrane enclosing a tiny sclerotized plate (Figs 99, 100); (2) a sclerite composed of two, lateral 'panels' that are joined medially and lie between the ends of the cardines (this arrangement can be envisaged as a flat sclerite that has become strongly infolded), postero-ventrally a narrow process curls forward below the halves and is separated by the interscleritic labial membrane from the prementum (Figs 101, 102). In other words, in (1) three separate sclerotized pieces can be distinguished (prementum + tiny, often triangular plate + larger, flat, sometimes sub-quadrate plate), whereas in (2) only two sclerotized pieces can be seen (prementum + infolded sclerite with process). I am cautious to apply specific terminology to these basal sclerites, but the most plausible interpretation is that in both (1) and (2) there is a single basal sclerite (i.e. the postmentum) and that in (1) the interscleritic labial membrane has developed a weak, medial, sclerotized section (a secondary development). Using Michener's (1984) approach, the tiny sclerotized piece in the membrane would be interpreted as a true mentum. The mentum is, however, a subdivision of the postmentum, whereas state (1) in *Scrapter* appears to be the scleritization of the interscleritic membrane

and not the subdivision of the postmentum. Ergo, the triscleritic complex of some *Scrapter* species is only convergently similar to the superficially similar state seen in the Apinae (Plant & Paulus 1987: figs 13-16).

An apparently intermediate condition between the two states is observed in *S. bicolor*. Here the sclerite between the cardine apices is moderately infolded and not a flat plate; but it is still separate from the small, triangular sclerite adjacent to the prementum (Fig. 103).

In those *Scrapter* species with state (2) there is variation in the structure of the dorsal portion of the sclerite. In *S. heterodoxus* the apical margin is emarginate and a protuberance is visible on the postero-dorsal surface that has squamous patterning (Fig. 104). In *S. caesariatus* Eardley there is an additional dorsal process extending out from the apical margin (Fig. 105).

In Hylaeinae, Xeromelissinae and Euryglossinae the postmentum is a small, flat, usually sub-quadrate plate (Fig. 106; Michener 1984: 709-710, figs 11-16; Plant & Paulus 1987: 86, fig. 2). The postmentum is separated from the prementum by the interscleritic labial membrane. Michener (1984: 709-710) interpreted the membrane to be a non-sclerotized mentum. The condition in the hylaeines and euryglossines is similar to state (1) described above for certain *Scrapter* species, with the exception that those taxa always have a part of the interscleritic labial membrane sclerotized. This scrapterine condition can easily be derived from that in the euryglossines and hylaeines, or vice versa. The postmentum in euryglossines, hylaeines and xeromelissines resembles that of sphecoid wasps (e.g. Plant & Paulus 1987: figs 20-23), and such a postmentum was argued to be the plesiomorphic condition for bees by Plant & Paulus (1987: 96-97). I agreed with this interpretation (plausibly making the euryglossines-hylaeines the most plesiomorphic bee lineage); but such a viewpoint is untenable in light of the molecular phylogenies of Danforth *et al.* (2006).

In the Colletinae (*sensu* Michener 2000), the postmentum is a well-sclerotized body with a narrow extension or process that curls underneath the basal section and is attached to the interscleritic labial membrane (Fig. 107; Michener 1984: 710, figs 17-20; Plant & Paulus 1987: 87-88, fig. 5). This condition agrees closely with state (2) described above for certain *Scrapter* species, and is illustrated for an unspecified *Scrapter* species by Michener (1984: figs 21-22), although an unsclerotized gap putatively separated the dorsal sclerite ('lorum') and posterior process ('mentum') in Michener's preparation. However, in our dissections, those *Scrapter* species with a state (2) postmentum, the dorsal sclerite and

posterior process are not separated. It is in state (1) that a three sclerite condition is observed.

The disparity in the structure of the postmentum of *Scrapter* was an unexpected discovery. Such a marked difference weakens belief in the monophyly of the genus. A thorough survey of the postmentum of as many colletid genera as possible (particularly of Australian and South American paracolletines) may cast further light on the evolution of the colletid postmentum.

Galea

The galea is the thin, distal-most sclerite of the maxilla. On its slightly concave inner surface, there is a row of bristles ('teeth') called the *galeal comb* arising on the base of the *inner rib of the galea* (Fig. 108). *Scrapter* has universally been held to have a small galeal comb consisting of fewer than five teeth (Cockerell & Ireland 1933: 973; Michener 2000: 127, 161; Ascher & Engel *in* Engel 2005: 13), although Friese (1909: fig. 19) illustrated *Polyglossa capensis* (= *S. capensis*) with a comb of approximately 15 teeth. Dissections for this study have revealed a range of comb sizes in the group. The number of teeth varies from 2-20 (Figs 109-114), and plotting all the values available as a bar graph shows a smooth continuum without any gaps. The teeth are generally slightly procurved and may be of equal length or increase in length proximally. The galeal comb is used to clean pollen off the forelegs (Jander 1976: 189; Krenn *et al.* 2005: 26).

There is a *line of sensilla* running parallel to the inner rib of the galea extending from the end of the galeal comb to the apex of the galea (Figs 108, 115). These sensilla are found in all scrapterines. On the ventro-medial section of the galea is the *sensory field* (Fig. 108) composed of sensilla similar to that in the sensillar line. The shape of the sensory field varies from species to species, and is greatly reduced in some (e.g. *S. flavipes* Fig. 116).

All *Scrapter* species possess the *galeal velum* (Fig 108). This is the thin, uppermost partition of the galea. There is notable variation in the outline of the velum: strongly tapering (*S. tomentum* Eardley, Fig. 108), weakly convex (*S. heterodoxus* Fig. 117), convex but emarginate distally (*S. amplitarsus* (Friese), Fig. 118), strongly convex (*S. algoensis* Fig. 119), broadly-rounded but falling short of the galeal apex (*S. absonus* Eardley Fig. 120), or narrow and largely parallel-sided (*S. amplispinatus* Fig. 121). The external surface of the galea below the galeal velum varies in surface sculpturing. In many

Scrapter species the surface is squamous (Fig. 122), but some have a smooth surface with no trace of roughening (Fig. 123).

Although significant attention has been given to bee glossal structure, the maxilla of 'short-tongued bees' has received far less treatment. The euryglossine galea (Figs 7, 124) is strongly divergent from that of *Scrapter*: the apex is abruptly truncate, there is no velum, the procurved galeal spine is present and the galeal comb stands apart from the main galeal sclerite on a robust, crescentic sclerite that is also connected to the sensory-field area. The hylaeine galea is similar to that of euryglossines (Fig. 125), but the velum is present and procurved galeal spine absent. The hylaeine galeal comb is also on a strong crescentic sclerite that is not closely contiguous with the inner galeal rib. In xeromelissines the galeal comb is reportedly quite weak, consisting of ten or fewer teeth (Michener 2000: 171). Other features of the xeromelissine galea are unknown to me. In a *Colletes* exemplar, from Lesotho, I observed that there are two separate ribs on the inner galeal surface (Fig. 126). The first (primary) rib divides the velum from the rest of the galea. The second (secondary) rib separates the galeal comb and sensory field from the main galeal sclerite. The galea of *Colletes* could be thought of as comprising three sclerites: 1) the lower-most, smooth, galeal comb-bearing sclerite, 2) the main galeal sclerite with squamous patterning, and 3) the velum. It is unclear whether this tripartite galea is universal in *Colletes*, or that I merely chose an unusual exemplar; this requires investigation. The galea in paracolletines such as *Leioproctus* (*Nodocolletes*) and *Paracolletes* is similar to that of *Scrapter*: the velum is present, and the galeal comb is closely associated with the inner galeal rib (Fig. 127). The galeal comb appears fairly well developed in most paracolletines with approximately 10-20 teeth (Fig. 127; Rayment 1954: figs 7, 8; Houston 1990: fig. 3i; Michener 2000: fig. 38-18a).

Interpretation of the diverse colletid galeae is not easy. An apparent transformation series exists leading from the triscleritic condition of *Colletes* to the euryglossines/hylaeines (where the lower-most sclerite bearing the galeal comb and sensory field has become partially associated with the main galeal sclerite), and finally *Scrapter* and the paracolletines (where the lower-most sclerite is completely attached to the main galeal sclerite and only distinguishable by its smooth surface), or vice versa.

Lacinia

I examined the lacinia in only four *Scrapter* species, but the variation shown was noteworthy. The lacinia in three species (*S. nitidus*, *S. chloris* and *S. bicolor*) was an

irregularly-shaped, weakly squamous to smooth sclerite, widest medially and tapering at the ends and positioned on the postero-dorsal margin of the galea and dorsal margin of the stipes (Figs 128, 129). The lacinia in *S. amplispinatus* was notably different being an elongate, largely parallel-sided sclerite (Fig. 130). The laciniae of colletids (and other bees) have been little described or illustrated in the literature. The laciniae in euryglossines and hylaeines are fairly large (in relation to galea), robust sclerites with strong setae; noticeably different from *Scrapter*. The lacinia in xeromelissines is described as a weakly-developed, almost hairless, elongate sclerite along the dorsal margin of the galea or stipes (Michener 1995: 333), but I am unaware of further details. In the paracolletine *Leioproctus* (*Nodocolletes*), I observed that the lacinia is a roughly triangular, smooth sclerite with strongly developed setae on the apical margin (Fig. 131). *Colletes* apparently lacks the lacinia altogether (Stephen *et al.* 1969: 9), which may be an apomorphic loss if consistent throughout that huge genus. A comprehensive SEM study of colletid laciniae would probably be a productive exercise.

Antennal sensilla

Ågren (1977, 1978), Ågren & Svensson (1982) and Ågren & Hallberg (1996) have comprehensively investigated the different types of sensilla found on the flagellomeres of bees. The distribution and conformation of these sensilla appears to be generally conservative across the bee clades and, hence, relatively uninformative from a phylogenetic perspective.

As far as I am aware, however, the antennal sensilla have only been documented for two genera of colletids, viz. *Colletes* and *Hyaleus* (Ågren 1977). To flesh out the corpus of data, a brief desription is provided here for female scrapterine bees.

The basal flagellomeres are thickly covered in sharp, simple setae (Fig. 132). From about F6 onwards, *plate organs* (*sensilla placodea*) become evident, as do occasional *pit organs* and *sensilla campaniformia*. The plate organs vary subtly in outline from circular to oval (Fig. 133) and are depressed medially. The pit organs are sunken circular features with a central hole bearing a slightly protruding, peg-like structure (Fig. 133). A variety of *trichoid sensilla* are present on the distal flagellomeres (Fig. 133). These range from long (15μm), thin setae (approximately 15X longer than broad) to shorter (5-8 μm), stubbier setae (approximately 5X longer than broad). Ågren (1977, 1978) and other authors have divided trichoid sensilla into different types, but classification is not easy and I have

merely termed them trichoid sensilla. On the final flagellomere (F10), there is a largely naked zone disto-ventrally (Fig. 134). Such a bare area is observed in other colletids (Ågren 1977) and Andrenidae (Ågren 1978).

Facial fovea

Schönitzer & Schuberth (1993) and Schuberth & Schönitzer (1993) have investigated the morphology of facial foveae in bees. They reported a facial fovea in the upper paraocular area in most 'short-tongued' bees, with an epithelial gland below the fovea (Schönitzer & Schuberth 1993: figs 10, 11). The fovea was found to be more strongly developed in females than males.

In *Scrapter* a fovea is present in all species (and both sexes), but there is considerable variation in its appearance. In some species (e.g. *S. nitidus* Fig. 135) there is a deep, narrow groove beginning slightly dorsad of the upper eye margin and running obliquely to about 1/3 down the length of the eye. The bottom of the groove cannot be seen and there are no setae in the groove. These facial foveae have a strong similarity to those of Hylaeinae and Euryglossinae (e.g. Houston 1975*b*: fig. 28; Schönitzer & Schuberth 1993: fig. 6; Exley 1996: figs 2-5). This trait is also reported in paracolletines like *Callomelitta* Smith and some *Eulonchopria* Brèthes (Michener 1965: 36, 1989: 669-670, 2000: 162).

In other species (e.g. *S. basutorum* (Cockerell)) the fovea forms a fairly well-defined ovoid bowl with smooth surface and no setae (e.g. Fig. 136), or is shallow with squamous patterning (e.g. *S. chloris* Fig. 137), or is indistinct, broad and poorly differentiated from the surrounding integument (e.g. *S. bicolor* Fig. 138).

Mandible

Michener & Fraser (1978) have extensively reviewed the mandibular structure of bees. In this study only the mandibles of female *Scrapter* species were investigated. The *Scrapter* mandible fits what Michener & Fraser (1978: 474) term the 'ancestral type of [bee] mandible' that is found in most ground-nesting bees (colletids to fideliids).

Figure 139 illustrates the features of the mandible. In *Scrapter* there is a single *pre-apical (sub-apical) tooth*. The *acetabular groove* is present (a few setae in the groove), ventrally the *acetabular groove* is separated from the narrow, deep *outer groove* by the smooth *outer ridge*. The *outer ridge* curves upwards proximally. The outer groove opens proximally where it becomes the *outer interspace*. The outer groove generally has many long, downward-curved, simple setae that become much shorter on the outer interspace.

The apex of the *outer groove* extends distally slightly further than the apex of the acetabular groove. The outer groove is separated from the *condylar groove* by the smooth, hairless *condylar ridge*. The condylar ridge forms the ventral-most edge of the mandible for most of its length and proximally joins the *mandibular condyle*. In the distal-most portion of the mandible, the *adductor ridge* curls round from the inner surface to terminate on the cap of the rutellum and thus constitutes the ventral-most edge of mandible distally. The *condylar groove* begins on the lower inner surface of the mandible but extends onto the outer surface anteriorly separating the condylar and adductor ridges. Distally the condylar groove extends weakly beyond an imaginary line dropped from the pre-apical tooth.

The inner surface of the mandible is dominated by a large proximal swelling, the *adductor convexity* (Fig. 140). The lower edge of the convexity is represented by the adductor ridge. Ventrally, the *condylar interspace* separates the adductor and condylar ridges. A line or shallow groove is present near the upper margin of the inner surface and is called the *fimbriate line*. Above the adductor convexity is the *trimma*, a gently sloping area covered in short setae. No clearly defined *trimmal carina*, separating the trimma and adductor convexity, is evident in *Scrapter*.

Within the Colletidae, the 'ancestral mandible' is observed in *Colletes* (Michener & Fraser 1978; fig. 2), paracolletines and Diphaglossinae (Michener & Fraser 1978: 474). The status in Euryglossinae is not discussed in Michener & Fraser (1978). Contrasting with other colletids, the twig- and cavity-nesting Hyaelinae and Xeromelissinae have modified mandibles. They are sub-triangular (i.e. broad at the base, tapering strongly to the apex) with an extremely broad *outer interspace* (Michener & Fraser 1978: fig. 5). These modifications presumably relate to their nesting habits. I am unaware of the mandibular structure in ground-nesting xeromelissines such as *Geodiscelis* Michener & Rozen. Michener & Rozen (1999: 3) merely reported (in *G. megacephala*) that the female has a 'strong pre-apical tooth', and Packer (2005: 88) observed that the female of *G. longiceps* has a 'small pre-apical tooth'. Michener & Fraser (1978: 474) described 'a broad, secondary, longitudinal median ridge in the adductor interspace' of the inner mandibular surface in *Colletes* (Fig. 141), *Amphylaeus* Michener and *Callomelitta* (weakly developed). This 'special and doubtless derived ridge' (Michener & Fraser 1978) is not seen in *Scrapter*.

Pronotum

Eickwort (1969: 344, fig. 30), McGinley (1986: 11, figs 9-12) and Engel (2000: 17-18, figs 30-31) have investigated pronotal ridges in halictid bees. I do not know of any detailed treatment of pronotal ridges in colletid bees. There is notable variation in the development of ridges and sulci on the pronotum in *Scrapter*.

The *lateral ridge of pronotum* begins on the dorsal surface of the pronotum and terminates on the sides of the pronotum (Fig. 142). The ridge is prominently developed and sharp-edged in some taxa (e.g. *S. tomentum*, *S. calx*), to weakly defined (e.g. *S. chloris*) or completely absent (e.g. *S. amplitarsus*) in others. A strong groove, the *lateral pronotal sulcus*, begins near the lateral ridge, runs obliquely down the side of the pronotum terminating near the mesepisternum (Fig. 142). The lateral pronotal sulcus marks off the *pronotal lobe* distinctly.

Prosternum

The prosternum is partly hidden ventrally by the procoxae and propleura. Three *Scrapter* species were examined, and some variation was encountered. In *S. bicolor*, *S. chloris*, and *S. nitidus* the *apophyseal pit* is largely hidden (Figs 143-145). The *median prosternal groove* is long and conspicuously pitted in *S. nitidus*, less strongly developed in *S. chloris* and is barely evident in *S. bicolor*. The *lateral processes* are long in *S. chloris* and *S. bicolor*, but shorter in *S. nitidus* (Figs 143-145). There are no detailed examinations of prosterna in colletid bees (or bees in general). A detailed investigation of the pro- and endosternum in bees would probably provide many points of phylogenetic value to melittologists.

Antenna cleaner (= *strigilis*)

Schönitzer (1986) has reviewed the structure of the antenna cleaner or strigilis in bees. The antenna cleaner is composed of two parts (Fig. 146): (1) the *strigilar concavity*, a comb-bearing notch on the postero-proximal section of the probasitarsus, and (2) the *malus*, a modified protibial spur. The malus consists of a thin, lamellate *velum* and a narrow, often squamate *trunk* that terminates distally in the *apex* (Figs 146, 147). A short row of seven to nine teeth (*apical row of teeth*) is present on the anterior edge of the apex. The apex is about 0.3-0.6X the length of the trunk. The velum is broadest distally and tapers proximally. The distal edge of the velum varies in *Scrapter*; it may be rounded (e.g. *S. amplispinatus*, Fig. 148), sharply pointed (e.g. *S. bicolor*, Fig. 147) or truncate (e.g. *S.*

capensis Fig. 149). The trunk is covered in pointed squamae, but varies from weakly (e.g. *S. amplispinatus*) to thickly covered (e.g. *S. bicolor*). On the postero-ventral margin of the malus is the *ventral row of teeth* (Fig. 150). This row is variably developed in *Scrapter*, the teeth being practically absent in some taxa (e.g. *S. chloris*) to well-developed in others (e.g. *S. nitidus*).

There is little literature on antenna cleaners in colletids. Schönitzer (1986: figs 1-2) illustrated two species of *Hylaeus* (= *Prosopis*), that showed pronounced intra-generic variation. The *Scrapter* antenna cleaner is similar, in broad terms, to that illustrated for *Hylaeus*. Schönitzer (1986: 47) averred that a plesiomorphic ('ancestral') antenna cleaner is characterised by a slender velum, long apex, squamous trunk and two rows of teeth. Most of these traits are displayed by *Scrapter* (and other colletid bees).

Pollen-collecting and grooming brushes

All *Scrapter* species of both sexes have *pro-, meso-* and *metabasitarsal posterior brushes*. These are dense brushes composed of short, simple setae on the underside of the basitarsi (Fig. 151), and are presumably for general grooming. There was no detectable variation in the structure of these brushes in *Scrapter*. The brushes agree with Braue's 'Bürstenhaare am ersten Tarsenglied' (Braue 1913: 86, figs 5 and 6).

On the anterior side of the probasitarsus there is another brush (Figs 151, 152). Eickwort (1969: 349) uses the term *anterior probasitarsal brush* specifically for a row of flattened setae on the outer edge of the probasitarsus in augochlorine halictids. This brush is not homologous with the brush seen in *Scrapter* and, hence, I refrain from using Eickwort's term, positionally descriptive as it is (perhaps Eickwort's brush should be renamed the *anterior probasitarsal pecten*, leaving the other term for more general use). The structure of the scrapterine brush varies. Some species have brushes comprising only simple setae (e.g. *S. basutorum* Fig. 152a), others only branched setae (e.g. *S. heterodoxus*, *S. bicolor* Figs 152b,c) and still others a combination of both (e.g. *S. luridus*). The diversity in structure of these brushes suggests a difference in function, presumably related to scraping pollen off the anthers (e.g. Houston 1990: 589; Michener 2000: 15; Müller & Kuhlmann 2003), or perhaps the cleaning of the underside of the head (Jander 1976: 183). Therefore differences in the structure of the anteriorly-positioned probasitarsal brush may be related to flower preferences (pollen structure) rather than any phylogenetic signal. The postero-distal portion of the protibia also has the same type of branched setae (in those species with branched setae), and is a continuation of this brush. The branched setae

present in these brushes approach Braue's group of 'Einseitig, gefiederte Haare' (Braue 1913: 89, figs 19 or 23). In South American *Leioproctus*, Michener (1989: 632) reported that the 'front basitarsus of female usually without well formed comb of setae on outer margin, but such a row of setae present in subgenera *Cephalocolletes*, *Nomiocolletes*, *Reedapis*, and *Spinolapis*'.

On the mid-leg, *Scrapter* has a strip of hair on the postero-distal section of the mesotibia, which is the *mesotibial comb* (Fig. 153). Jander (1976: 187) restricted the term to the Halictidae and Andrenidae, noting 'on the mesotibia of Colletidae no conspicuous brush or comb is found'. Michener (2000: 48), Engel (2001: 35) and others have used the term 'mesotibial comb' more broadly. The *Scrapter* mesotibial comb is appreciably less pronounced than that seen in halictids (pers. obs.). Opposing the mesotibial comb and mesobasitarsal posterior brush is a comb-like strip of hair on the proximo-ventral part of the mesofemur and mesotrochanter (Fig. 154). Thus, a mesotrochanter-mesofemur/mesotibial-mesobasitarsal coupling is achieved for the cleaning of the foreleg (see Jander 1976: 184-186 for discussion).

Pollen is packaged into scopae on the hindlegs and also on sternum 2 in *Scrapter*. The *hindleg scopa* is most strongly developed on the metatibia, where a thick mass of plumose setae is present. The metatibial scopa is divided into two sections (Fig. 155): a dorsal ridge of dense, stout, branched setae (near fig. 23 of Braue (1913)) and an antero-lateral swathe of long, softer, palmate setae (near figs 25/26 of Braue (1913)). The antero-lateral section represents the primary pollen-holding setae. Stockhammer (1966: 183-184) observed that the dorsal serrated and claw-like (simple, curved) setae on the metatibia of ground-nesting augochlorine halictids serve as support 'when the tibiae are pressed against the walls of a tunnel'. His observations suggest that the dorsal ridge of stiff setae has a different (or additional) function from the softer, antero-lateral setae. Further, pollen is more weakly represented on the dorsal ridge than on the antero-lateral section. In other words, the rigid, dorsal metatibial setae may serve as aids to the crampon-like metabasitibial plate in navigating nest tunnels. On the posterior face of the metatibia are simple, longish setae, which are the *keirotrichia* ('shorn setae'). Short keirotrichia are widespread in bees and wasps, but Michener (1989: 628) suggested long keirotrichia may be an apomorphy for the paracolletine genus *Leioproctus*. This is possibly a synapomorphic resemblance between *Scrapter* and *Leioproctus*, but the nature of keirotrichia in euryglossines and other colletid bees is barely mentioned in the literature.

Keirotrichia are apparently used to clean the wings (Michener 2000: 48; see also Jander & Jander 1978).

The anterior part of the metafemur has a curtain of downward-hanging, plumose setae (Fig. 156). These setae abut a naked, smooth area that lies on the antero-ventral side of the metafemur and is the 'corbicula' of Michener (2000: 130), or more precisely the *fiscina* (Engel 2001: 28).

The metatrochanter has a ventral fringe of long, plumose setae (the branches are concentrated distally on each hair and approach setae in fig. 23 of Braue (1913)), and evidently it forms part of the functional scopa (Fig. 156). The metacoxa also has a ventral fringe of soft, minutely plumose bristles, but the setae are different from those of the metatrochanter, and the metacoxal setae do not form part of the functional scopa. The metabasitarsus has the usual grooming brush posteriorly. Antero-dorsally it has a few, curved, stiff, branched setae, but these are of feeble importance for the scopa. Thus, in summary, the scopa in *Scrapter* on the hindleg is (in terms of importance): metatibia + metafemur + metatrochanter (+ metabasitarsus). The pollen grains packaged into the scopa are always dry i.e. never moistened with nectar.

An important ancillary part of the scopa on all *Scrapter* species examined is the presence of plumose setae on the sterna, mainly S2. In females loaded with pollen, these sterna are always packed heavily with pollen. That the sternal setae are 'scopal' is also indicated by the absence of plumose setae on S2 in males. Alexander & Michener (1995, character 93) coded a sternal scopa as absent in *Scrapter* (using *S. heterodoxus* as their exemplar), but this is incorrect. A sternal scopa is also found in some South American paracolletines (Michener 1989: 630), but seemingly not in any other colletids.

Scopae are absent in euryglossines and hylaeines which transport pollen internally (the setae on the metatibiae are simple in these bees, excluding the apical metatibial 'penicillus'). There have been few dedicated studies on scopae in scopa-bearing colletid bees. Pasteels & Pasteels (1976) investigated the scopae of colletids using scanning electron microscopy. They emphasised the diversity of scopal types in the colletids, and re-affirmed the belief that the nudity of hylaeines and euryglossines was secondarily derived, because they presumed scopae would be ineffectual in tiny bees ('...rappelons que ce sont des insectes de petite taille, chez lesquels une scopa formée d'une couverture de soies ne serait probablement pas efficace' Pasteels & Pasteels (1976: 99)). Their treatment was rather generalised, and the scrapterines approach most closely the scopae described for the Colletinae (e.g. Pasteels & Pasteels 1976: figs 18-20). Michener (1989: fig. 19) illustrated

representative setae from the 'lower part' of the metatibial scopa in South American paracolletines. *Scrapter* most resembles the tibial setae illustrated for *Leioproctus* subgenus *Perditomorpha* Ashmead and, to a lesser extent, *Leioproctus sensu stricto*.

Mesocoxa

Michener (1981*a*) studied the middle coxae of bees (and some 'sphecids') and found that the mesocoxa of bees forms a vertically elongated spindle divided into two unequal halves: a large *basicoxite* and a small *disticoxite*. The bees were also divided into two groups: those with hemicryptic mesocoxae (i.e. most of basicoxite withdrawn under the pleuron) and those with mostly exposed mesocoxae. Melo (1999: 18) showed that the basicoxite is absent in bees and sphecoid wasps, but did not propose any new terminology for the divided coxa. Within the colletid clade, all groups have a hemicryptic mesocoxa with the putative exception of the euryglossines and xeromelissines (Michener 1981*a*: 321). In *Scrapter* the mesocoxa is hemicryptic with a fairly strong *mesocoxal carina* (Fig. 157).

Metabasitibial plate

The metabasitibial plate is used for gaining purchase while the bee moves along the tunnels of the nest or fashions the brood chambers (Batra 1964; Stockhammer 1966: 183; Michener 2000: 32, 48). Differences in metabasitibial plate structure may relate to differences in nesting substrate.

The metabasitibial plate varies greatly amongst the *Scrapter* species. All *Scrapter* species (of both sexes) have metabasitibial plates. Eardley (1996: 57) stated that the plate is absent in female *S. avius*, but this is incorrect. In some the plate is vestigial, replaced by a ring of tubercles delimiting the original margin of the plate (Fig. 49). In others the plate is entire i.e. a complete, smooth-edged, slightly elevated plate (Fig. 158) that is rounded or slightly pointed distally. A range of intermediate conditions occur. The plate may be largely entire with the margin notched (Fig. 159b), or consist of a posterior carina with tubercles anteriorly (Fig. 159c), or merely a posterior carina alone (Fig. 159d). A variable number of setae (5 to >100) arise from the plate. The setae are usually simple, but bifid ones are sometimes present. In some species (e.g. *S. albifumus*, *S. calx* Eardley, *S. armatipes* (Friese) Fig. 159a) the plate is densely hirsute such that it may be almost completely obscured.

There can be substantial sexual dimorphism in the plate, e.g. *S. bicolor* male has a half-entire metabasitibial plate with only the posterior carina present. In the female the

posterior carina is largely reduced to approximately four tubercles with another three anteriorly. In some other species (e.g. *S. albifumus*) the plates are similar in both sexes.

Pretarsal claws and associated structures

The pretarsal claws are either simple (e.g. Fig. 160) or variably toothed (Figs 161-164). When toothed, the pre-apical (sub-apical) tooth is shorter than the outer tooth (the pre-apical tooth varies from ½ to ¾ of the length of the outer tooth). The pre-apical tooth may be rather blunt (Fig. 162) or sharp (Fig. 163); this is possibly wear-related.

Two long, tapering setae arise on the proximo-ventral section of each pretarsal claw, as discussed by Michener (1944: 183) and Eickwort (1969: 350). These two setae appear to be found in all bees, although in *Apis* only one seta is present (Erickson *et al.* 1986: 152). These setae are here termed *paired, proximal ungual setae*, and vary in conformation in *Scrapter*. For most *Scrapter* species both setae are simple, spirally-grooved setae (Figs 161-164; near fig. 12 of Braue (1913)). In a minority of taxa, the more basal seta is spirally grooved and the outer seta branched (Fig. 160; near fig. 18 of Braue (1913)), or both are branched (Fig. 165).

The *orbicula* (manubrium of Snodgrass (1956) and Eickwort (1969)) is a sclerite that occupies the space between the distitarsus and arolium (Fig. 166). This sclerite tapers distally and is covered in approximately 7-10 setae. The two distal-most setae are significantly longer than the other setae and usually weakly plumose (e.g. *S. capensis*, *S. chloris*, *S. niger*, *S. bicolor*) or simple (e.g. *S.* cf. *erubescens* Fig. 164).

The *unguitractor plate* is a sub-quadrate sclerite covered largely in squamous spicules (Fig. 167). Medially the spicules become more tapered and seta-like. Along the distal edge of the plate are approximately 10 short, simple setae. The base of the plate (i.e. proximal edge) is notched medially (as noted by Michener 1944). The unguitractor plate is uniform in all *Scrapter* species examined (Fig. 167). Indeed, an examination of the unguitractor plate in exemplars from other bee clades (melittids, halictids, fideliids) shows uniformity in appearance. Of potential significance, however, the bee unguitractor plate differs from that of sphecoid and vespoid wasps examined (which have hairy or spiculate plates). A squamous unguitractor plate may be a synapomorphy for the bees; this conjecture requires corroboration.

The *planta* is a sub-quadrate sclerite lodged between the pretarsal claws and furnished with approximately 40-50 short setae. In most *Scrapter* species the setae are simple (Figs 167, 168), but in certain taxa the setae are distinctly branched (Fig. 165).

Sternum 8

Eardley (1996: 38) and Ascher & Engel (*in* Engel 2005: 13) noted that in *Scrapter* the male S8 is elongate with the apex of the distal process protruding externally, and superficially recalling a pygidial plate. This characteristic is observed in all *Scrapter* males, although the amount of the S8 protruding varies. The S8 is internalised in most other colletids, but in the paracolletine *Leioproctus* (Colletinae *sensu* Michener) a similar condition is observed: 'S8 with apical process ending in rounded, beveled area that is exposed at rest and resembles a pygidial plate' (Michener 1989: 632). Figure 169 shows the protruding S8 in male *S. heterodoxus*.

Pygidial plate

The pygidial plate is used to tamp or pound soil in the brood chambers (Batra 1964, 1968: 124; Stockhammer 1966: 183; Michener 2000: 32). The pygidial plate is found in all female scrapterines. It tapers gradually distally with a rounded tip, is hairless and has smooth edges. Several species of male scrapterines also have a pygidial plate (Fig. 169, *contra* Ascher & Engel *in* Engel 2005). The pygidial plate is particularly well-developed on the male of *S. heterodoxus* (Fig. 169), less so in other males bearing the plate.

Sting apparatus

The sting apparatus is an intricate structure enclosed by T6 and S6. The final terga (T7 and T8) have become internalised (the corresponding sterna have apparently been lost), and become intimately associated with the sting. Each tergum is divided into two halves, which are unconnected in bees. The sting apparatus is weakly sclerotized in *Scrapter*, and the details are not easily discerned using light microscopy.

Packer (2003) has comprehensively reviewed the sting apparatus across all the major bee clades, and illuminated a range of structural diversity. Packer related some of that structural diversity to phylogeny, but did not discuss the implications for colletid phylogeny in any substantial detail. Toro (1973) and Aravena & Toro (1985) have investigated parts of the sting (particularly T7 and T8) in the paracolletine *Leioproctus* and xeromelissines. Aside from these studies, and the data provided by Packer (2003), the sting morphology of colletids is largely undescribed.

Terminology for the parts of the sting apparatus has varied from author to author (e.g. Snodgrass 1956; Packer 2003; Rightmyer 2004). The terminology used by Rightmyer (2004) and Grimaldi & Engel (2005) is adopted here.

Tergum 7 is largely similar in the scrapterines examined. It is a pair of sub-quadrate, spiracle-bearing, weakly sclerotized sclerites. Features of the sclerite are labelled in Figure 106. The lateral and medial portions of the *marginal ridge* taper shortly before the posterior edge. The *spiracle* is laterally-positioned in the posterior half of the sclerite (Figs 170, 171). The posterior edge is straight (e.g. *S. chloris*) to weakly curved (e.g. *S. niger* Fig. 171b). The anterior edge is weakly to strongly curved (Figs 171a-d). The *apodemal process* may be weakly to strongly produced (Figs 171a-d). *Scrapter* lacks the *digitiform process* of Euryglossinae, although Packer (2003: 14) reported 'a similar but flatter structure in *Scrapter*'. Unlike the Euryglossinae, the spiracle is not posteriorly-positioned, i.e. opening onto the posterior edge (Packer 2003: fig. 3c). Tergum 7 of *Scrapter* is strongly divergent from those illustrated for *Hylaeus* (Hylaeinae) and *Chilicola* Spinola (Xeromelissinae) (Packer 2003: figs 3d-3e).

Tergum 8 is a pair of largely transparent, kidney-shaped sclerites, each divided into two sections by a *medial carina* (Fig. 172). The *condylar ridge* or condylar ridge area is straight to strongly curved in scrapterines (Fig. 172). The *gonangulum* (*first valvifer*) is a small, triangular sclerite that articulates with tergum 8 dorso-posteriorally. In *S. chloris* the *dorsal angle* has two distinct articulation points, but in other scrapterines there appears to be only one point. The *second gonocoxa* (*second valvifer*) is confluent with the *gonoplac* (*gonostylus*) and lies adjacent to the actual sting shaft. The *apodeme of the second gonocoxa* is approximately 0.75-1X breadth of the gonocoxal body. The *furcula* is a thin, Y-shaped sclerite (Fig. 173). In *Scrapter* species examined there is much variation in the relative lengths of the *dorsal* and *ventral arms*. In *S. chloris* the dorsal arm is 0.5X the length of the ventral arm, but in *S. nitidus* and *S. heterodoxus* the dorsal arm is approximately equal in length to the ventral arm. The ventral arms are widely splayed (large angle between arms). The dorsal arm is strongly laterally compressed. Packer (2003: fig. 11e) illustrated *Colletes*, where the ventral arms are moderately splayed and much longer than the dorsal arm (ventral arms 8X length of dorsal arm)

CHAPTER 5

CLADISTIC ANALYSIS

As alluded to in the 'Historical Review of *Scrapter*' (Chapter 1.3), Eardley (1996) divided *Scrapter* into eight species-groups that he suggested were 'conglomerates of species that share similar characters' (Eardley 1996: 37). Conversely, Michener (2000: 162) proposed two broad groupings based on differences in the facial fovea of female, metabasitibial plate of female, propodeal triangle sculpture, pretarsal claws, and the presence of tergal hair bands. Despite this division into two groups, Michener (2000: 162) admitted that 'a minority of species...break down the differences'. Further, Melo & Gonçalves (2005: 157) and Engel (2005: 13) have both advocated subdivision of *Scrapter* into an unspecified number of subgenera. These contrasting viewpoints are evaluated here via a preliminary, exploratory phylogenetic investigation of *Scrapter*.

5.1. Justification for character selection

Operationally, my first source of characters was Eardley's (1996) revision. Eardley essentially employed about 20 characters in his species descriptions and dichotomous key. I have used several of his characters except those representing autapomorphies for respective species, or those that were difficult to partition into discrete character states. Further, I took cognizance of the broader bee literature, especially that relating to colletid bees (e.g. Michener 1986, 1989; Alexander & Michener 1995) for additional characters. Characters in this study are based on adult morphology. Larval characters were not considered because larvae are only known for *S. niger* (McGinley 1981). Characters used and their states are provided in Table 4.

5.2. Cladistic Procedure

Out-group selection was problematic as the sister-group of *Scrapter* is uncertain, although a close relationship to the euryglossine and hylaeine bees is suggested (see 'Review of Colletid Relationships and Classification' above). Because of uncertainty surrounding *Scrapter* relationships several out-groups were used: Euryglossinae (*Euryglossa* sp.),

Colletes sp. (from Lesotho), and Hylaeinae (*Hylaeus* (*Euprosopis*) sp.). Table 5 summarises the distribution of character states among the taxa. Maximum parsimony was perfomed using Hennig86 version 1.5 (Farris 1988) (commands m*; bb*). Successive weighting was applied using commands m*; bb*; xs w; repeatedly until the output stabilised.

5.3. Cladistic results and discussion

Using equally-weighted characters more than 2000 most parsimonious trees were found. The consensus tree was very poorly resolved. Three characters (4, 6, and 11) were coded as additive to assist in resolution. Again more than 2000 most-parsimonious trees were found (length = 167 steps, consistency index = 35, retention index = 61). The strict consensus of these trees is shown in Fig. 175. This consensus tree is not fully resolved, but shows several subclades. The poor resolution is attributable to the low characters/taxa ratio and the missing values in the matrix, because of some taxa being known from only one sex. Applying successive-weighting resulted in >2000 most-parsimonious trees (length = 246 steps, consistency index = 56, retention index = 81). The strict consensus tree produced from these equally parsimonious trees was rejected because the euryglossine and hylaeinae exemplars were embedded within *Scrapter*.

To aid in improving resolution, I deleted the taxa only known from one sex and also *S. thoracicus* and *S. fuliginatus*, which had been scored from the literature due to the extreme paucity of material. Using equal-weights, 36 most parsimonious trees were recovered (length = 162 steps, consistency index = 37, retention index = 60). The strict consensus tree is shown in Fig. 176. Applying successive-weighting, 722 most parsimonious trees emerged (length = 232 steps, consistency index = 58, retention index = 78). The strict consensus tree produced a fairly well-resolved cladogram (Fig. 177). Of interest, five of the sub-clades were similar in both the equally-weighted and successive-weighted consensus cladograms using a reduced matrix.

The poor resolution and low CI values demand caution when interpreting the results. The cladograms are defensible, though, in this formative phase of phylogenetic comprehension of these bees. I am confident that the subclades identified will be shown to be robust by future analyses, as they accord with my intuitive perception of monophyletic groupings.

The first clade of note is here termed the *nitidus*-clade. This clade agrees with Michener's (2000) second grouping of elongate, largely nude bees having narrow facial foveae, simple metabasitibial plates and reticulate carinae on the basal area of the propodeal triangle (e.g. Eardley 1996: fig. 2). Some of these features show variation in this clade e.g. *S. opacus* has the carinae on the propodeal triangle much reduced (Eardley 1996: fig. 10). The inclusion of *S. heterodoxus* in the successive-weighting consensus tree (Fig. 177) is intuitively objectionable. On phenetic grounds, *S. heterodoxus* is noticeably dissimilar to the other clade members (being a large, robust, hairy bee with conspicuous tergal hair bands). Similarities, though, include the form of the labrum, postmentum structure and the presence of a medio-longitudinal clypeal suclus. With more data, *S. heterodoxus* may turn out to be the sister-group to the *nitidus*-clade. All of the taxa in this clade (including *S. heterodoxus*) visit the flowers of composite plants (Asteraceae, Table 1).

The second clade is the *erubescens*-clade predicated on the unique synapomorphy of a propodeal triangle with sharply incurved lateral margins. The three species in this clade are large-bodied, hairy bees (Fig. 72), and I am intuitively confident of their monophyly, but sister-group relationships are far less certain. The sister-group relationship to the *nitidus*-clade indicated in the successive-weighting consensus tree is not compelling.

The third clade is the *chloris*-clade comprising three taxa (*S. chloris*, *S. luridus* and *S. whiteheadi*). These are medium-sized bees with orange metasomas and a reduced clypeus in known males. Members of this clade are only known to visit *Grielum* flowers (Table 1).

The remaing subclades and relationships indicated in the successive-weights tree are not intuitively compelling. Further investigation of the relationships of these taxa is required.

The cladistic results provide only partial support for the divisions proposed by Eardley (1996) and Michener (2000). Some of Eardley's species-groups (e.g. the *erubescens* species-group) receive support, but others (e.g. the *S. bicolor* species-group) do not. Although Michener (2000) diagnosed what I have called the *nitidus*-clade, his partitioning of *Scrapter* into two groupings is too simplistic. Classificatory rearrangements are not proposed here. Although subdivision of *Scrapter* into a variety of subgenera has been advocated by other authors, the low consistency indices for the cladograms and the lack of unique synapomorphies for the different subclades makes subdivision an

unwarranted course of action for now. In particular, the type species for *Scrapter* (*S. bicolor*) appeared in a variety of positions.

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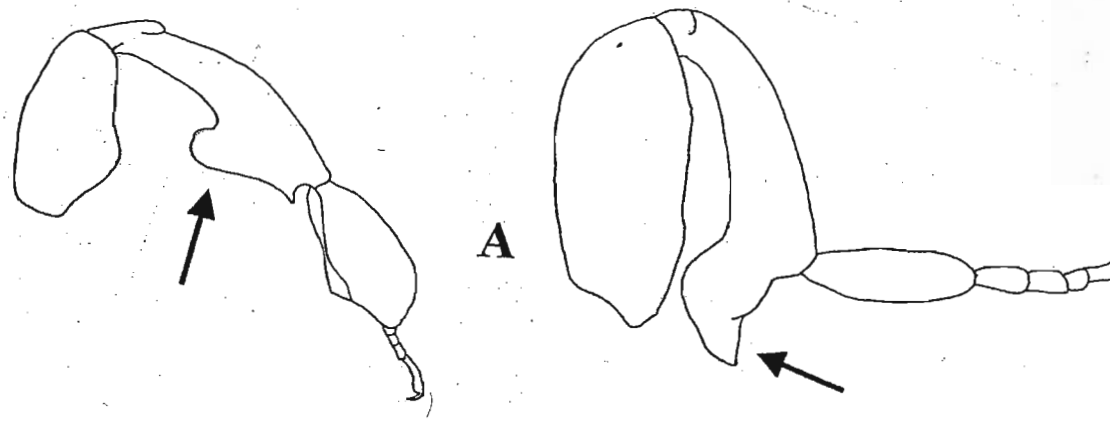
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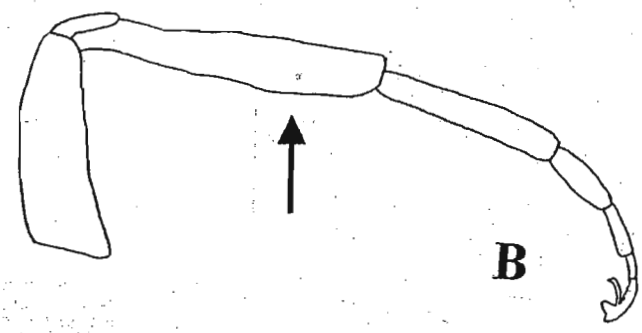
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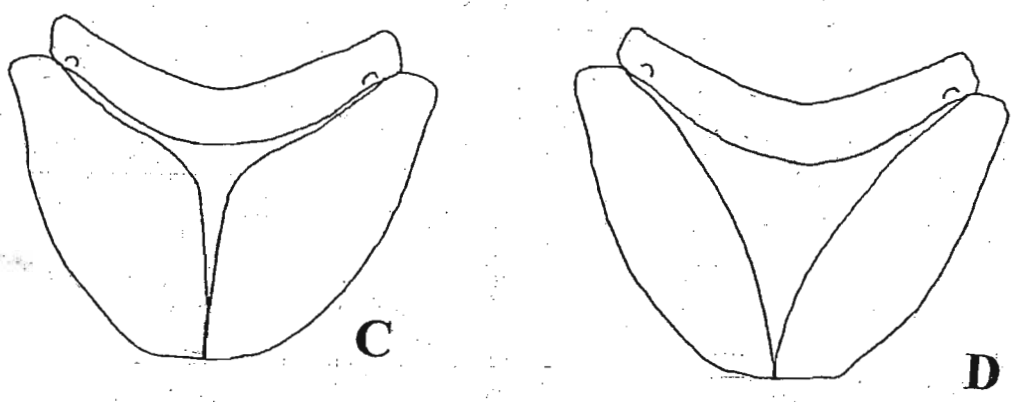
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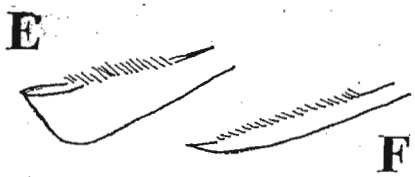
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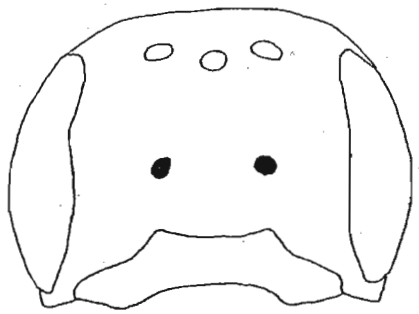

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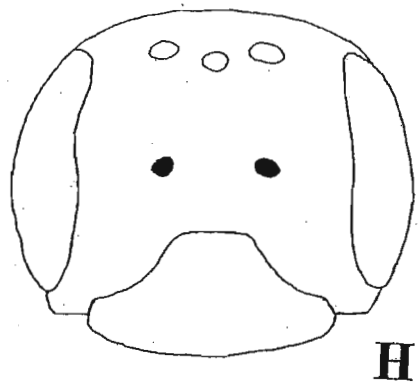

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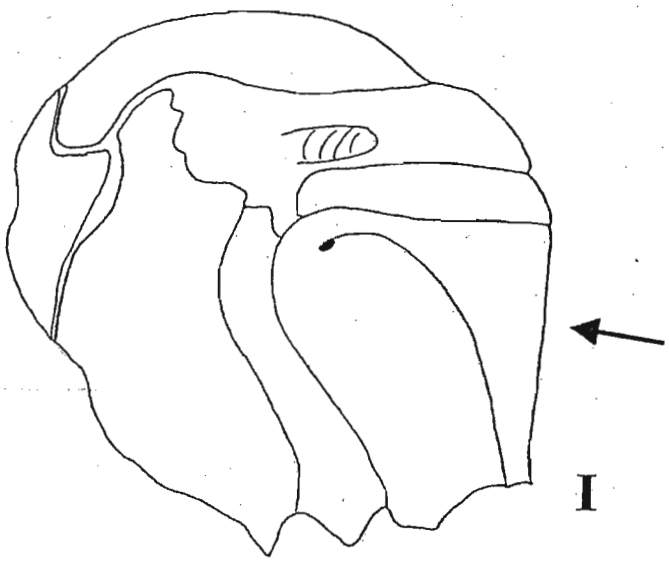

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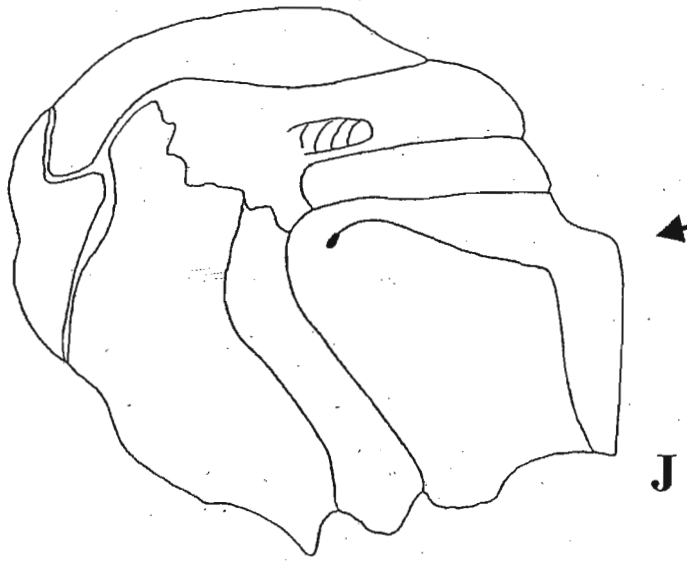

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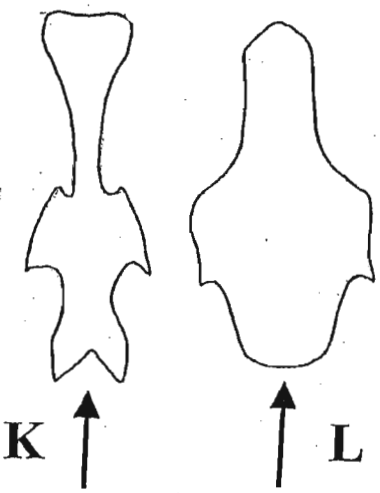

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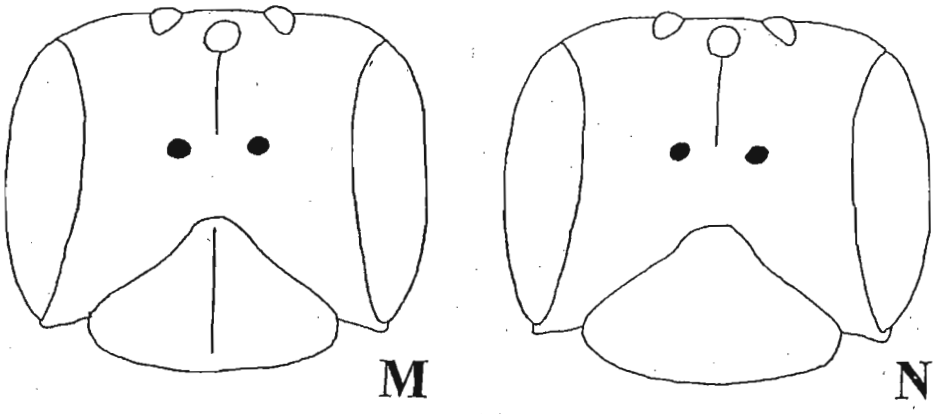
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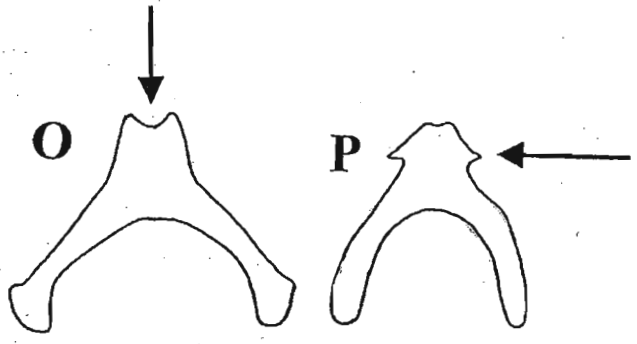
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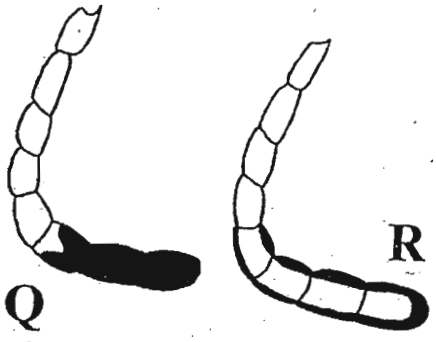
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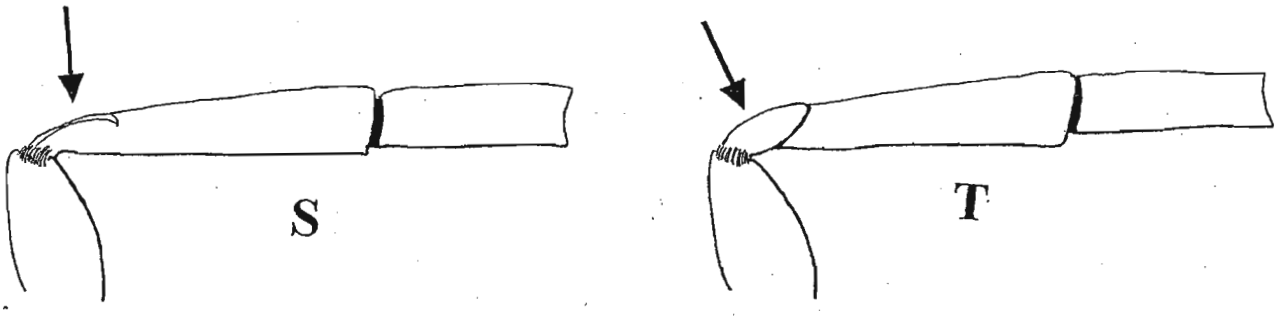
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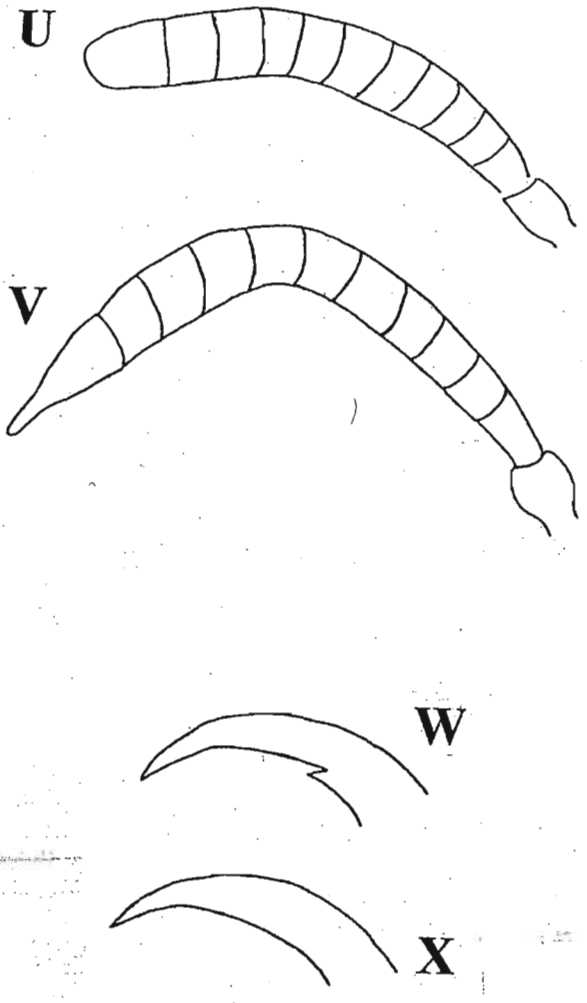
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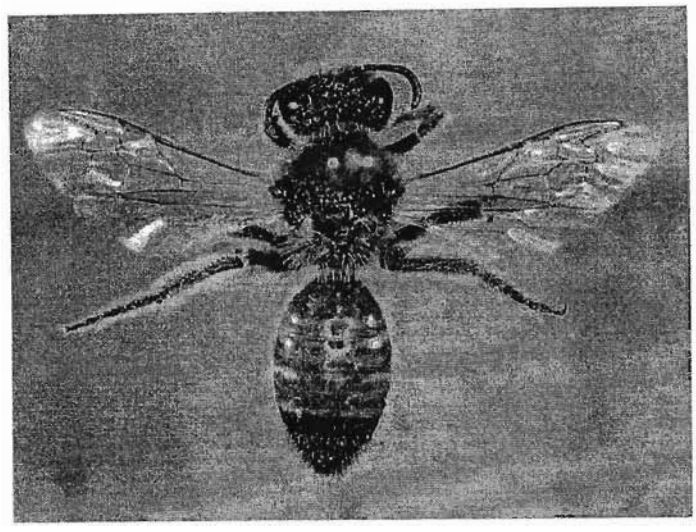
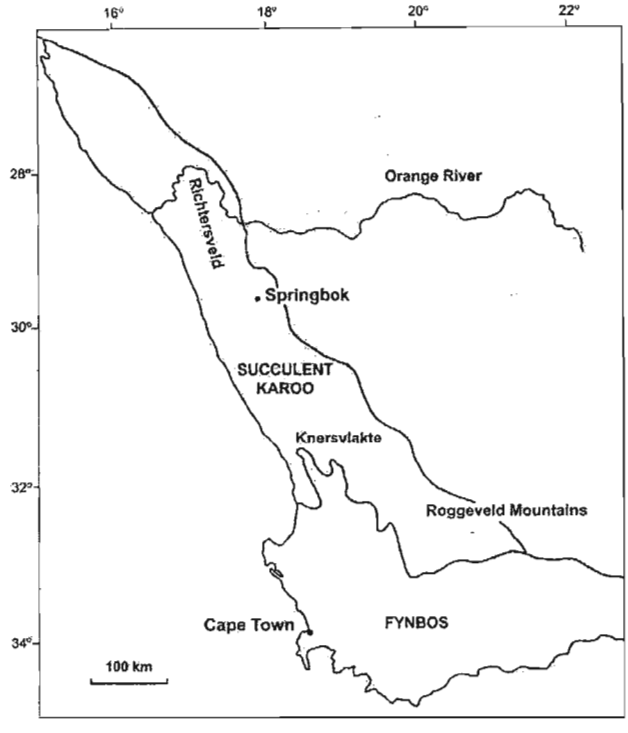




Figs 1-2. (1) Dorsal view of female *Scrapter luridus* Eardley; (2) Map of western South Africa showing the Succulent Karoo and Fynbos biomes, and several important localities mentioned in the text. The interdigitation of the two biomes has been greatly simplified in the map.

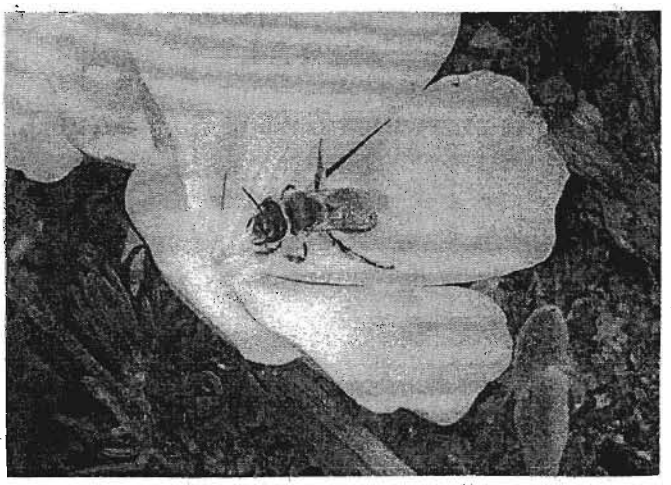


Fig. 3. *Scrapter chloris* Eardley female collecting pollen from flower of *Grielum* species.

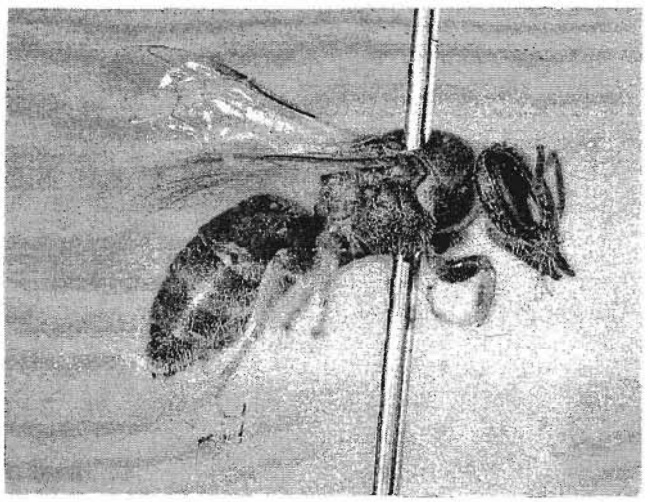


Fig. 4. Lateral view of *Euryglossula* sp. (Euryglossinae).

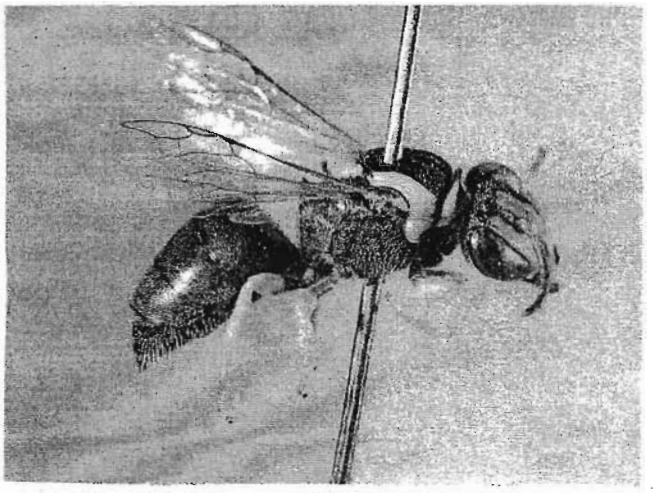


Fig. 5. Lateral view of *Hylaeus* sp. (Hylaeinae).

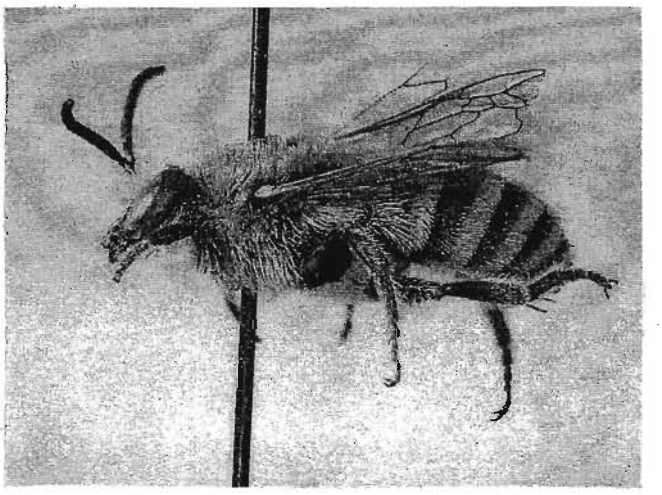


Fig. 6. Lateral view of *Colletes* sp. (Colletinae).

Table 2. Comparison of rank-based classifications recently proposed for colletid bees.

Michener (2000)	Melo & Gonçalves (2005)	Engel (2005)
COLLETIDAE	COLLETINAE	COLLETIDAE
Colletinae (incl. *Scrapter*)	Colletini	Colletinae
	Paracolletini	Paracolletinae
	Scrapterini[1] (*Scrapter*)	Scraptrinae (*Scrapter*)
Euryglossinae	Euryglossini	Hylaeinae
Hylaeinae	Hylaeini	Euryglossini
Xeromelissinae	Xeromelissini	Hylaeini
		Xeromelissini
Diphaglossinae	Diphaglossini	Diphaglossinae
Caupolicanini		Caupolicanini
Diphaglossini		Diphaglossini
Dissoglottini		Dissoglottini
-	-	Stenotritinae[2]

[1]Name nomenclaturally unavailable (Ascher & Engel 2006)

[2]Michener (2000), Melo & Gonçalves (2005) and Danforth *et al.* (2006) exclude the stenotritines from the colletid clade

Table 3. Summary of the taxonomic history of *Scrapter*.

Name	Type species	Remarks
Scrapter Lepeletier de Saint-Fargeau & Audinet-Serville, 1828	*Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, by designation of Vachal 1897: 63 (not *S. lagopus*, *vide* Cockerell (1920a: 254))	-
Polyglossa Friese, 1909	*Polyglossa capensis* Friese, by designation of Cockerell 1921: 203 (not *P. albitarsis* Friese, *vide* Sandhouse (1943: 589))	Made a subgenus of *Scrapter* by Cockerell (1934). Formally synonymised by Eardley (1996:38)
Strandiella Friese, 1912	*Strandiella longula* Friese, by designation of Cockerell (1916: 430)	Synonymised with *Scrapter* by Cockerell (1932a)
Parapolyglossa Brauns, 1929	*Polyglossa heterodoxa* Cockerell, by designation of Sandhouse (1943: 584)	Included in *Scrapter* by Eardley (1996: 39), but not formally synonymised

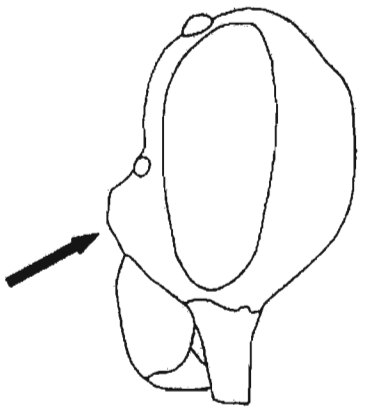
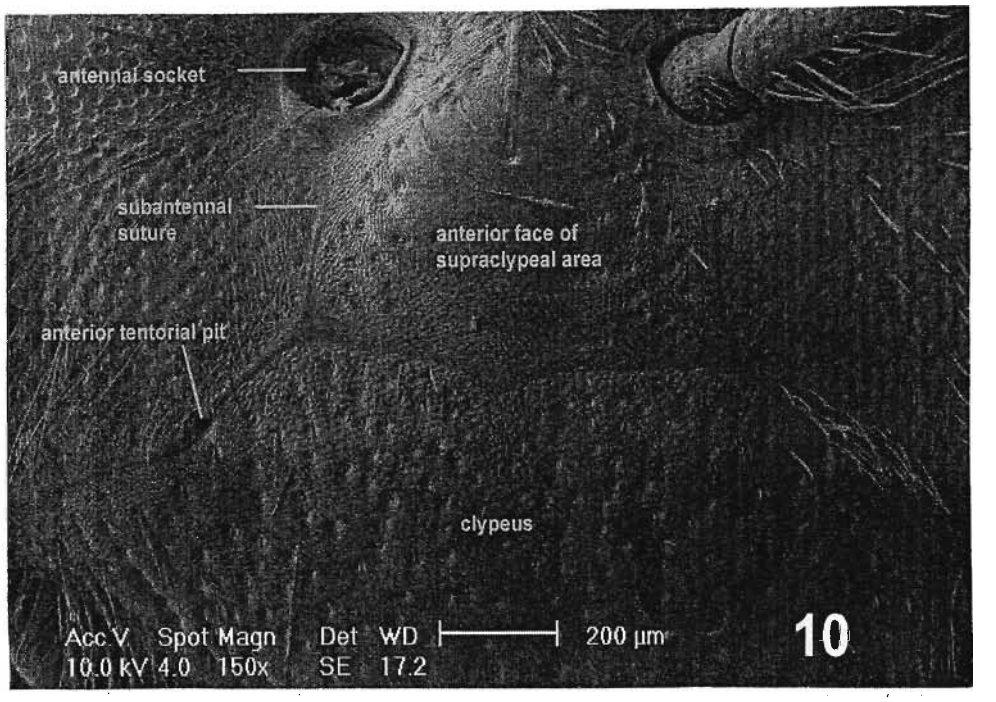
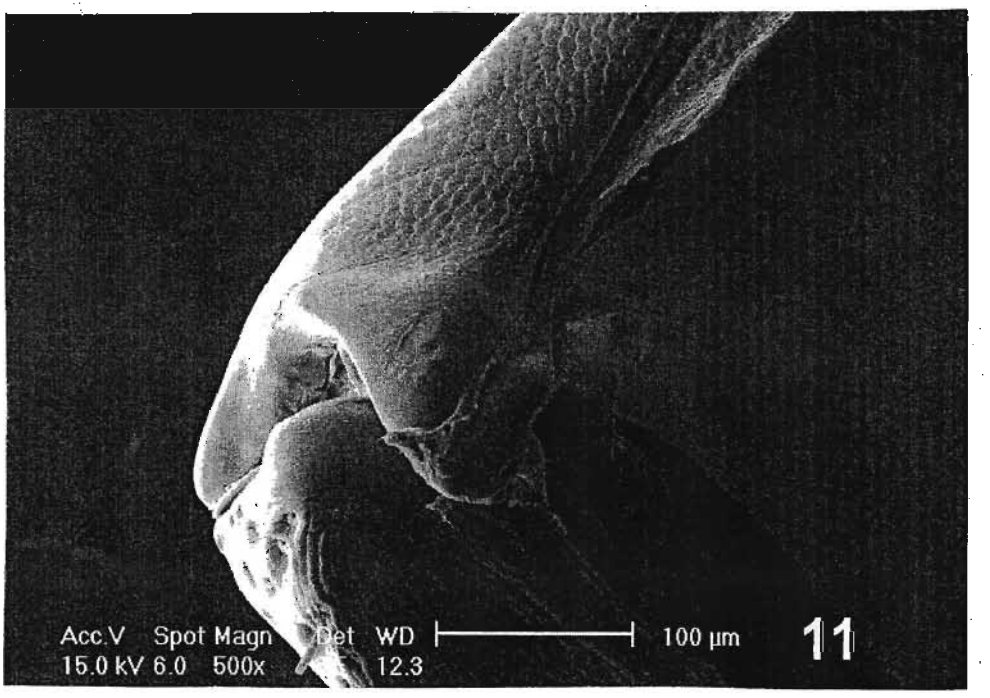
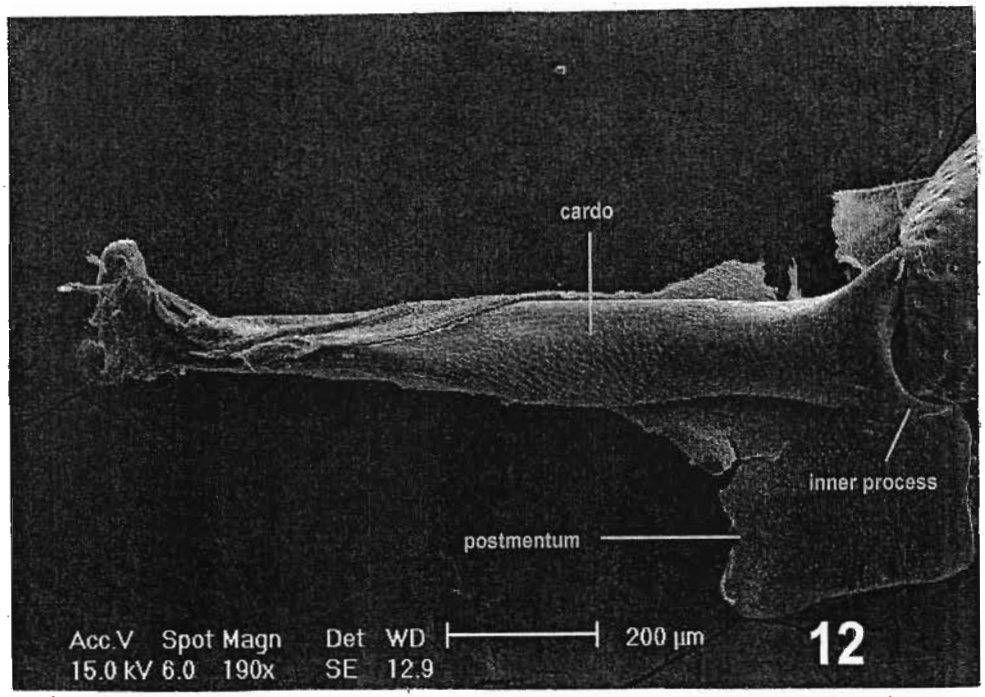


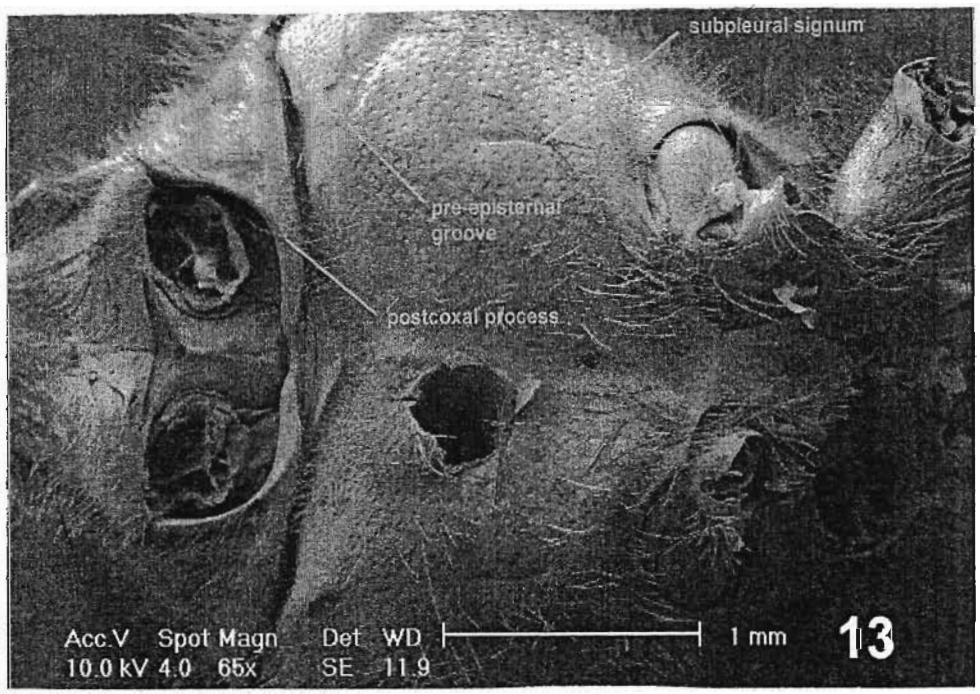
Fig. 9. Lateral view of diagrammatic *Scrapter* head showing bulbous supraclypeal area and anterior face of supraclypeal area (arrowed).



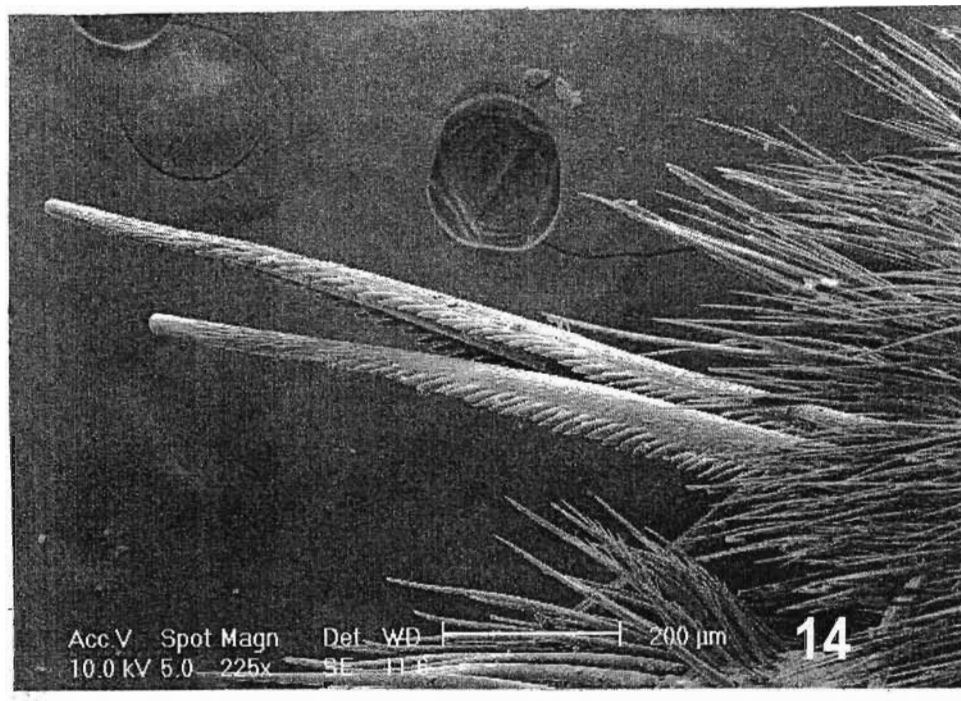


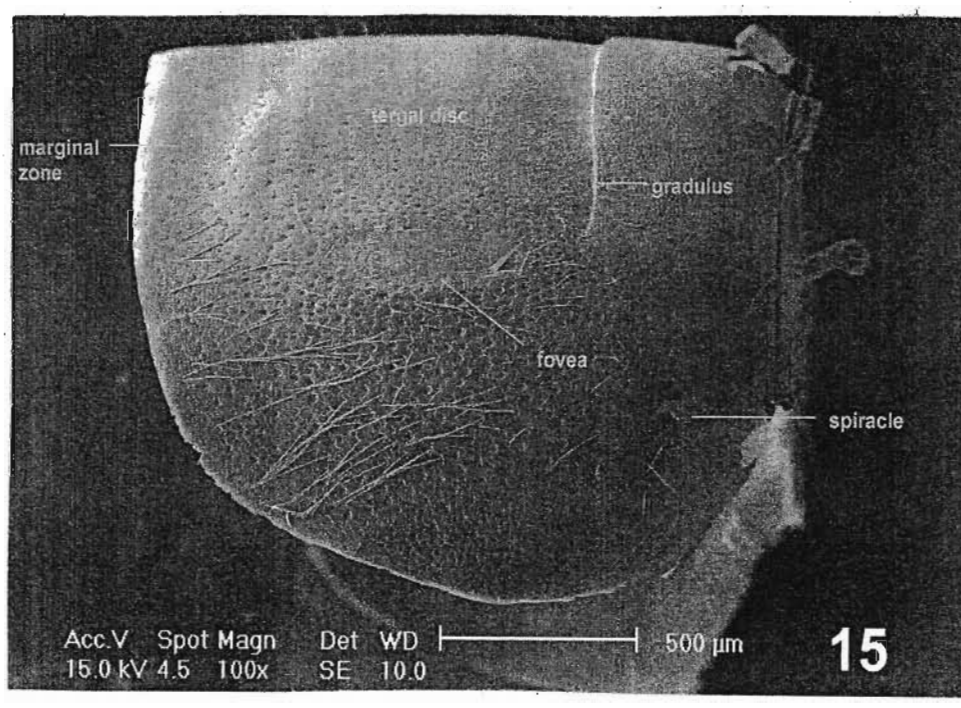
Figs 10-11. (10) View of *S. chloris* Eardley face showing clypeus, supraclypeal area and associated features, (11) Distal end of cardo (inner view) articulating with stipes.





Figs 12-13. (12) Posterior view of entire length of cardo, (13) Ventral view of *Scrapter chloris* Eardley mesosoma showing termination point of pre-episternal groove.





Figs 14-15. (14) Metatibial spurs of *Scrapter chloris* Eardley showing ciliate teeth, (15) Lateral view of tergum 2 of *Scrapter chloris* Eardley showing fovea.

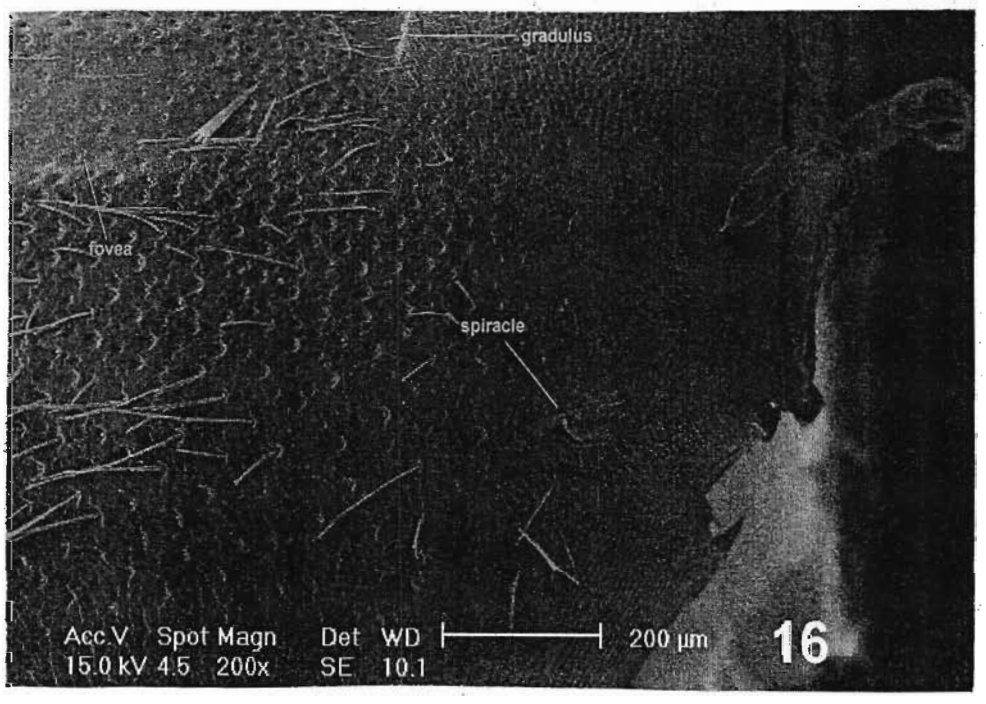
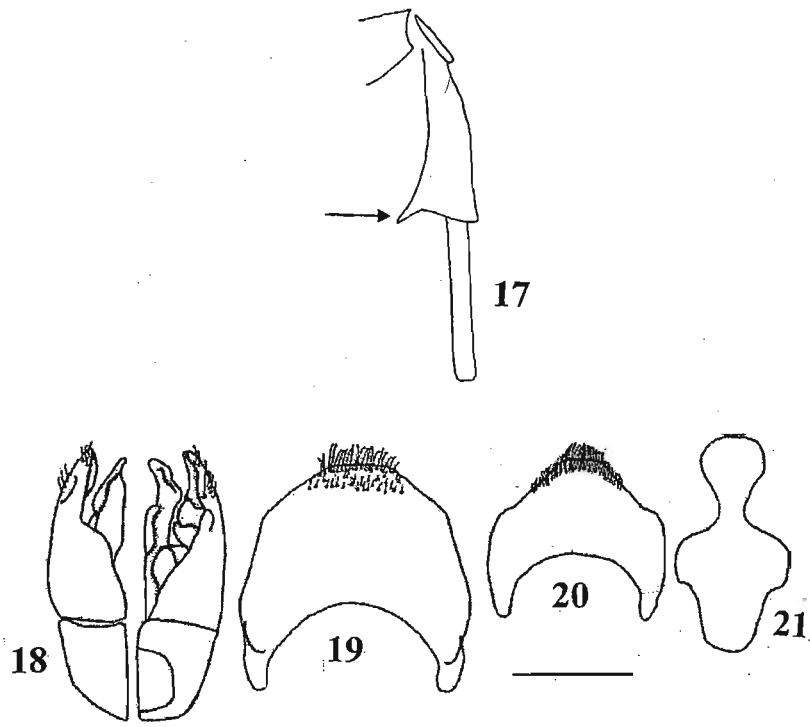
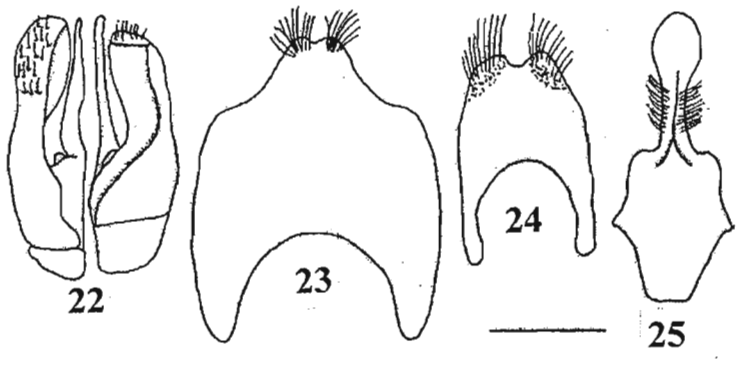


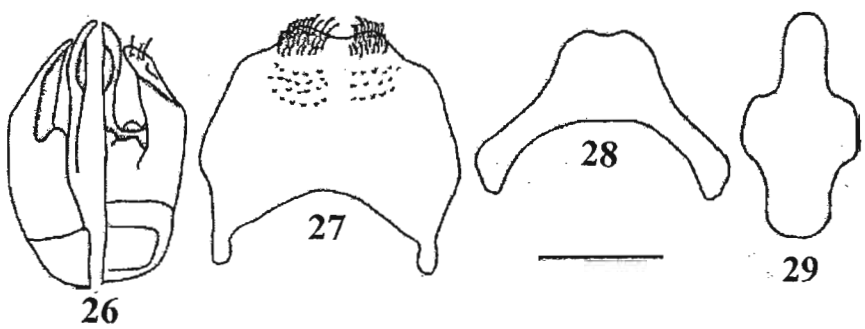
Fig. 16. Lateral view of tergum 2 of *Scrapter chloris* Eardley showing fovea in relation to spiracle and gradulus.



Figs 17-21. *Scrapter acanthophorus* sp. n., (17) distinctive spurred metatibia (arrowed) (18) genitalia (dorsal and ventral views), (19-21) S6-S8. Scale bar = 0.4 mm.



Figs 22-25. *Scrapter carysomus* sp. n., (22) genitalia (dorsal and ventral views), (23-25) S6-S8. Scale bar = 0.4 mm.



Figs 26-29. *Scrapter catoxys* sp. n., (26) genitalia (dorsal and ventral views), (27-29) S6-S8. Scale bar = 0.4 mm.

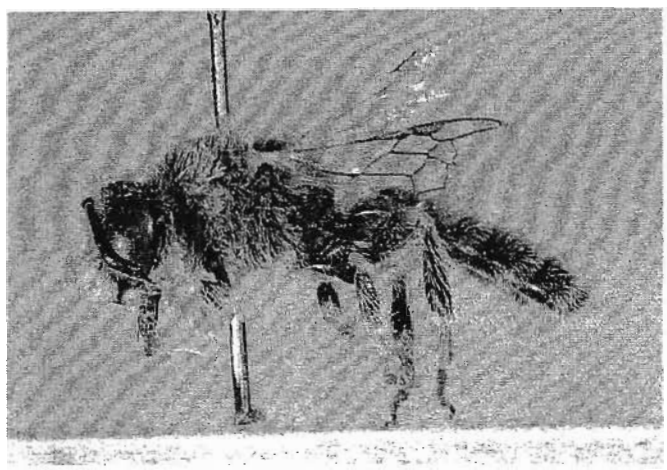


Fig. 30. *Scrapter catoxys* sp. n., lateral view of male.

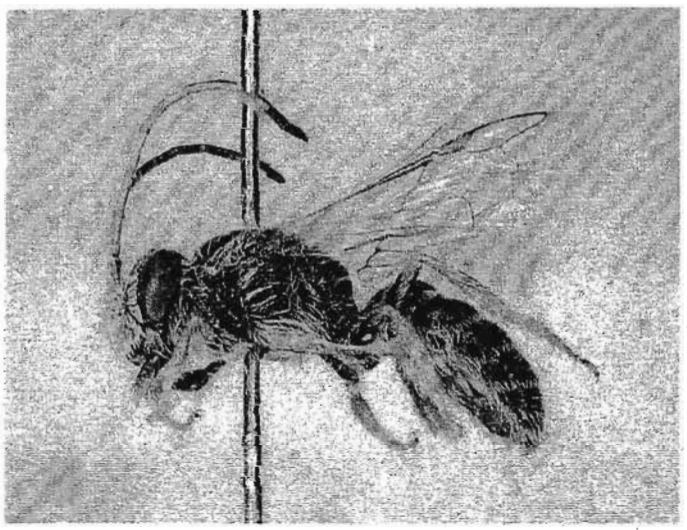
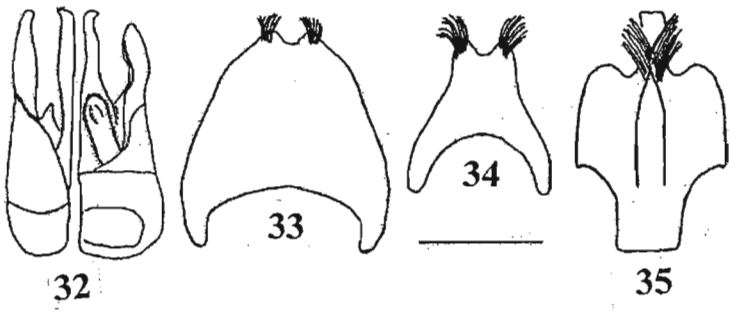
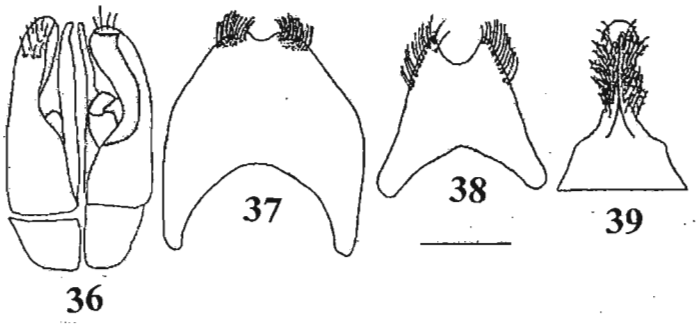


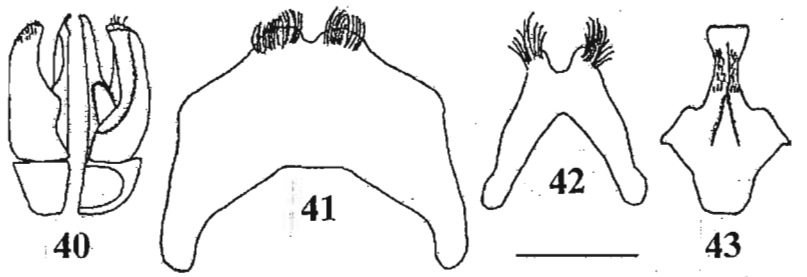
Fig. 31. *Scrapter chrysomastes* sp. n., lateral view of male. Note the extremely long antennae.



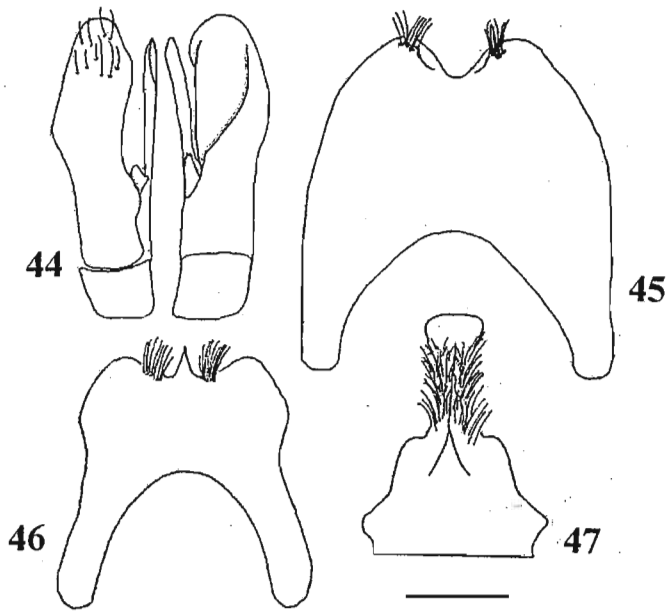
Figs 32-35. *Scrapter chrysomastes* sp. n., terminalia: (32) genitalia (dorsal and ventral views), (33-35) S6-S8. Scale bar = 0.4 mm.



Figs 36-39. *Scrapter eremanthedon* sp. n., terminalia: (36) genitalia (dorsal and ventral views), (37-39) S6-S8. Scale bar = 0.4 mm.



Figs 40-43. *Scrapter glarea* sp. n., terminalia: (40) genitalia (dorsal and ventral views), (41-43) S6-S8. Scale bar = 0.4 mm.



Figs 44-47. *Scrapter oxyaspis* sp. n., terminalia: (44) genitalia (dorsal and ventral views), (45-47) S6-S8. Scale bar = 0.4 mm.

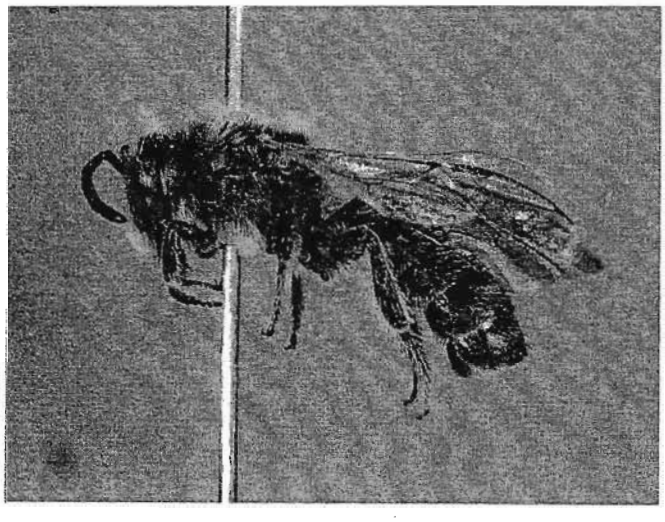


Fig. 48. *Scrapter oxyaspis* sp. n. lateral view of holotype.

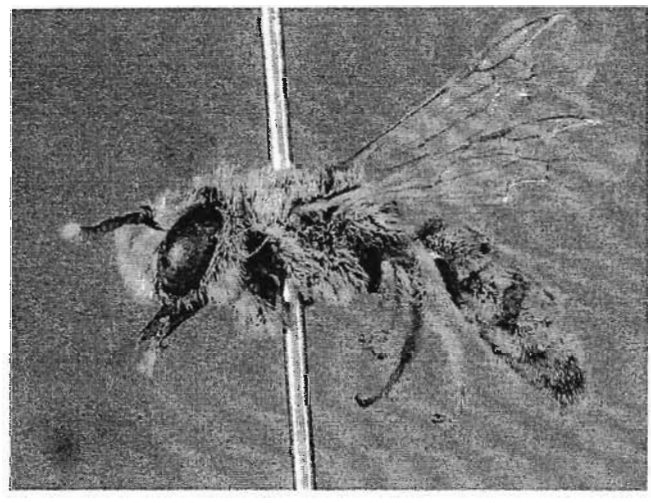


Fig. 49. Lateral view of male *Scrapter pruinosus* sp.n.

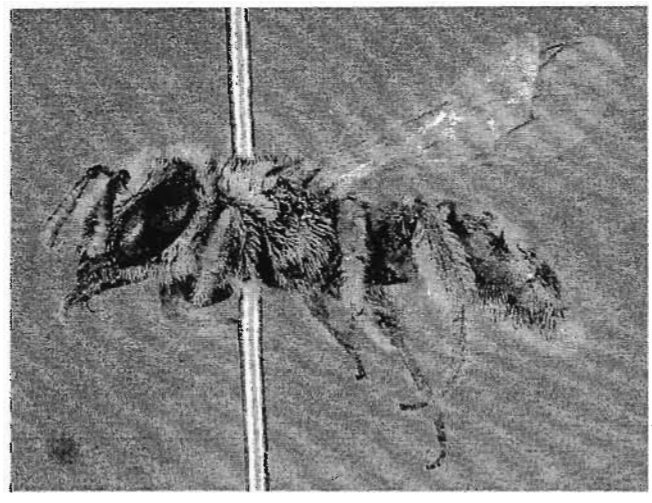


Fig. 50. Lateral view of female *Scrapter pruinosus* sp.n.

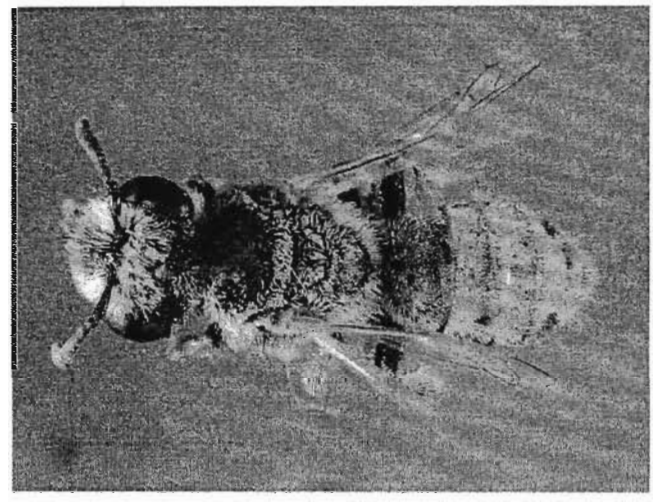
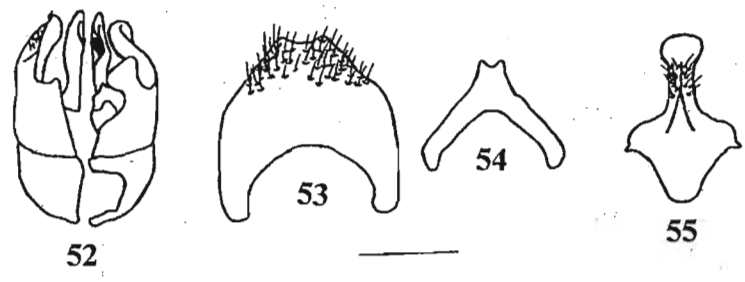
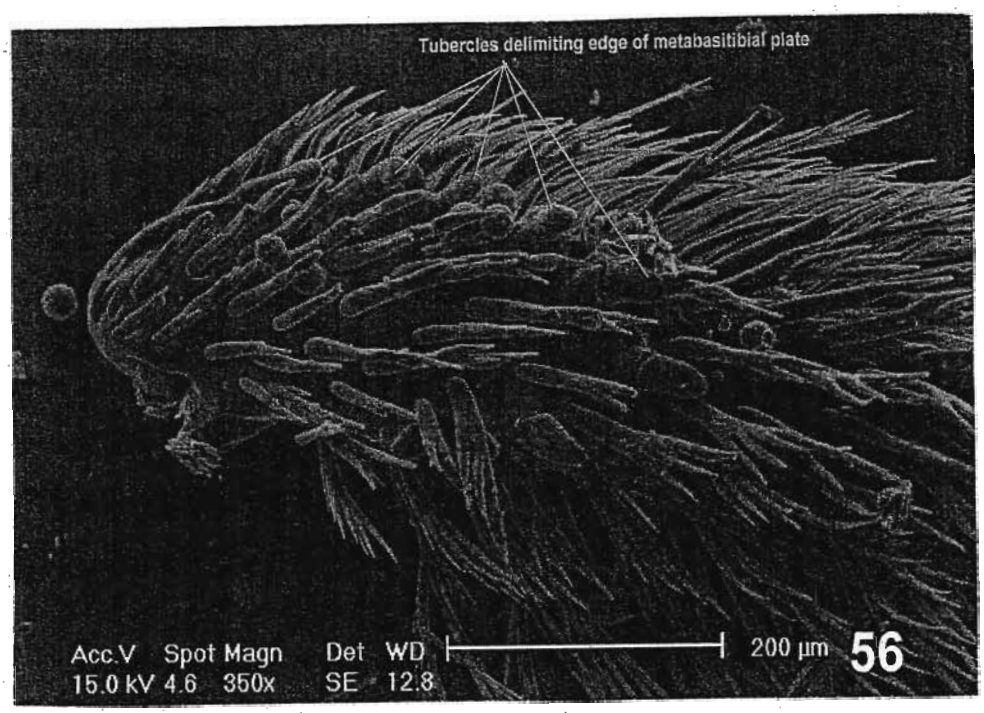
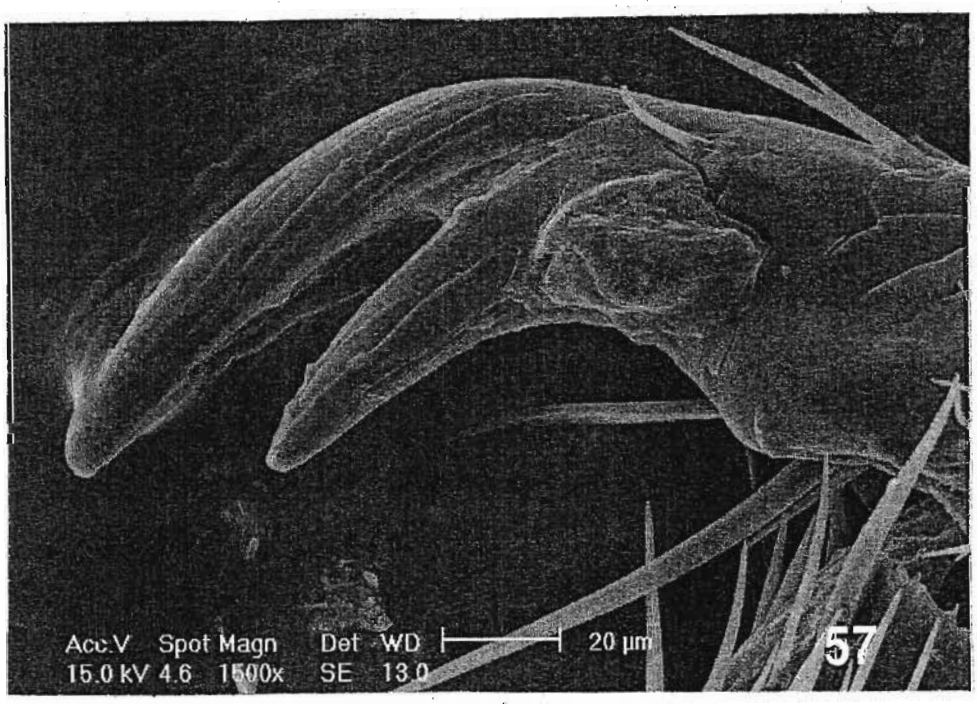


Fig. 51. Dorsal view of female *Scrapter pruinosus* sp.n.

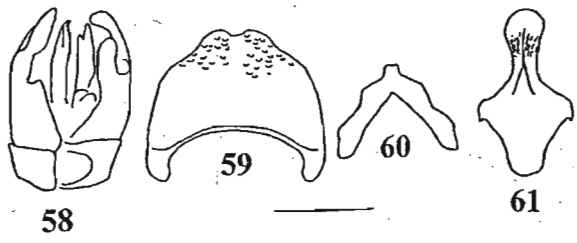


Figs 52-55. *Scrapter pruinosus* sp. n., terminalia: (52) genitalia (dorsal and ventral views), (53-55) S6-S8. Scale bar = 0.4 mm.





Figs 56-57. (56) Metabasitibial plate of female *Scrapter pruinosus* sp. n., note the tubercles delimiting the edge of the plate, (57) Pretarsal claw of female *Scrapter pruinosus* sp. n., note the cleft nature of the claw.



Figs 58-61. *Scrapter pyretus* sp. n., terminalia: (58) genitalia (dorsal and ventral views), (59-61) S6-S8. Scale bar = 0.4 mm.

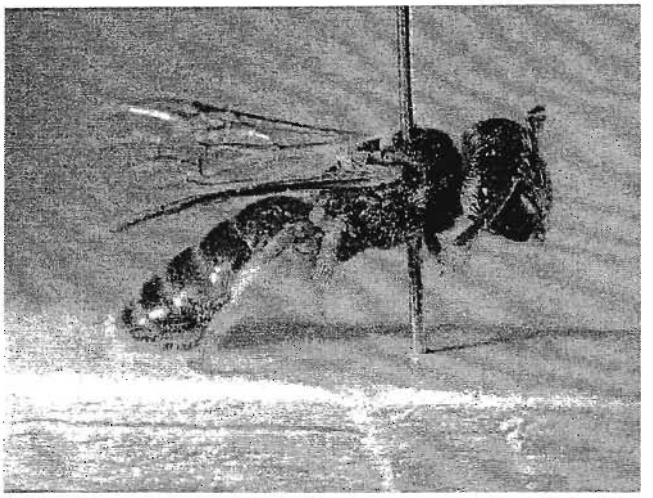
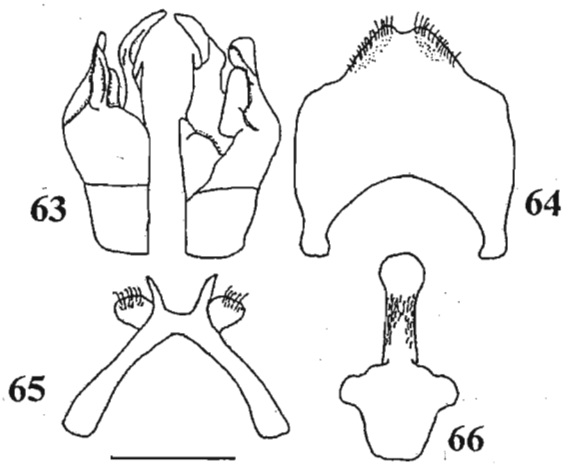
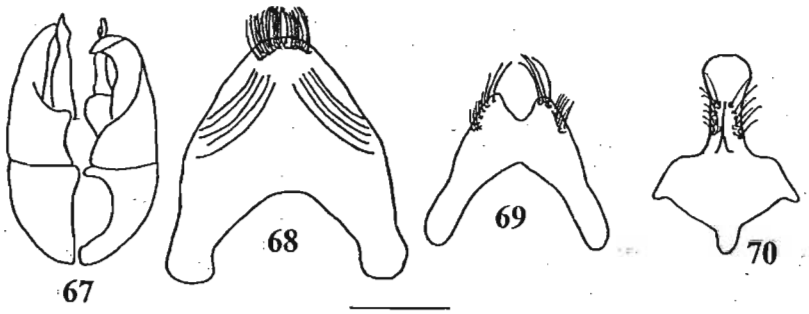


Fig. 62. Lateral view of female *Scrapter pyretus* sp. n.



Figs 63-66. *Scrapter sittybon* sp. n., terminalia: (63) genitalia (dorsal and ventral views), (64-66) S6-S8. Scale bar = 0.4 mm.



Figs 67-70. *Scrapter viciniger* sp. n., terminalia: (67) genitalia (dorsal and ventral views), (68-70) S6-S8. Scale bar = 0.4 mm.

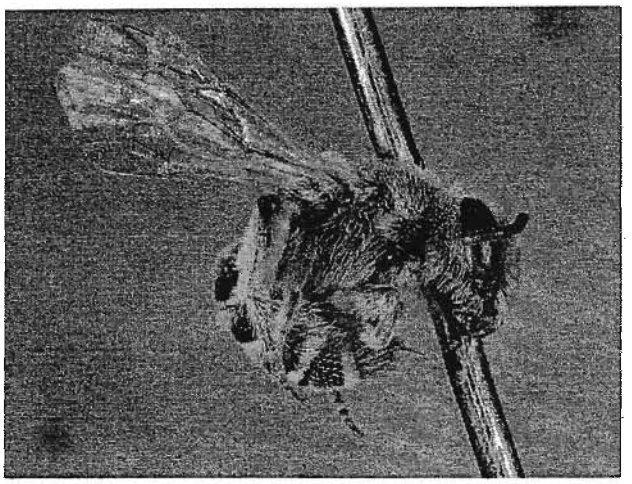


Fig. 71. *Scrapter albifumus* Eardley, lateral view of female showing characteristic curled posture on pin.

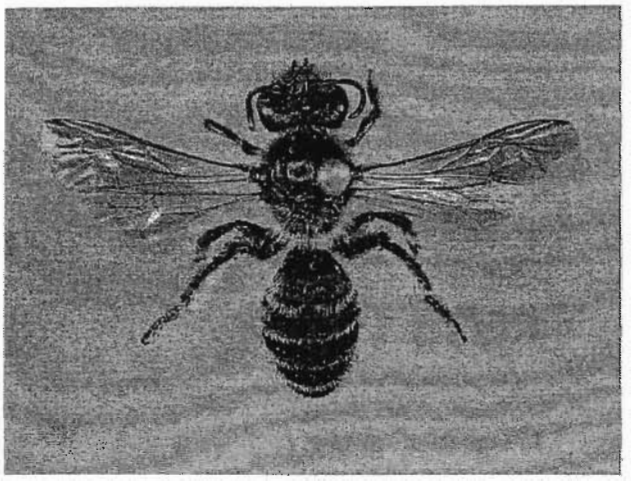


Fig. 72. *Scrapter amplispinatus* Eardley, dorsal view of female.

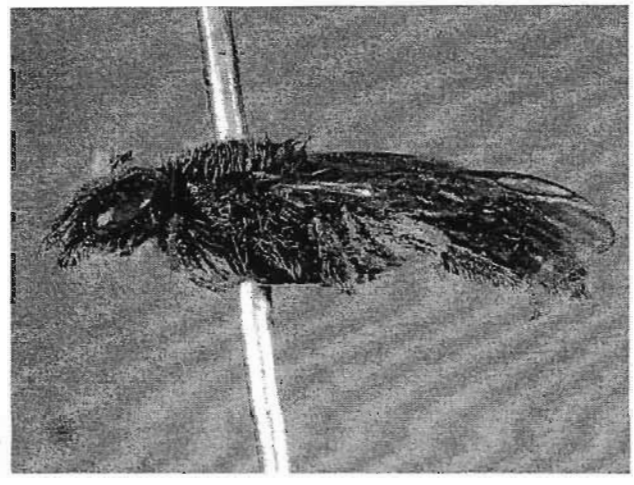


Fig. 73. *Scrapter niger* Lepeletier de Saint-Fargeau & Audinet Serville: lateral view of syntype of *S. subincertus* Cockerell.

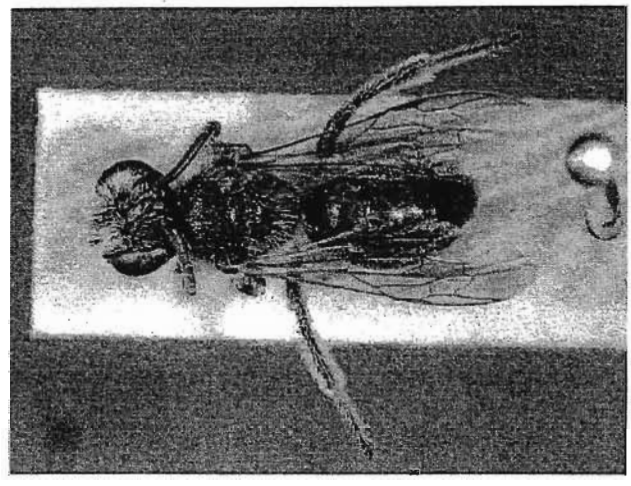


Fig. 74. *Scrapter niger* Lepeletier de Saint-Fargeau & Audinet Serville: dorsal view of *S. brunneipennis* Cockerell syntype.

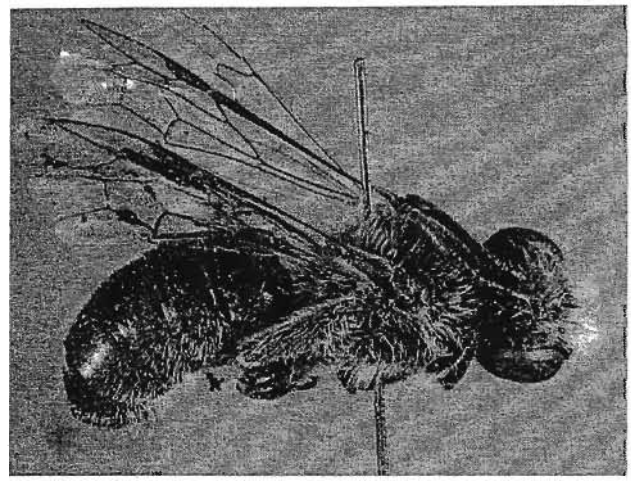


Fig. 75. *Scrapter leonis* Cockerell: lateral view of *S. merescens* Cockerell syntype

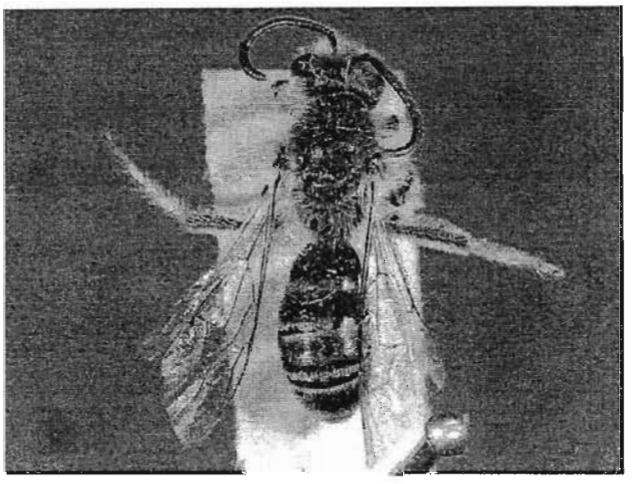


Fig. 76. *Scrapter algoensis* (Friese): dorsal view of *S. sinophilus* Cockerell syntype.

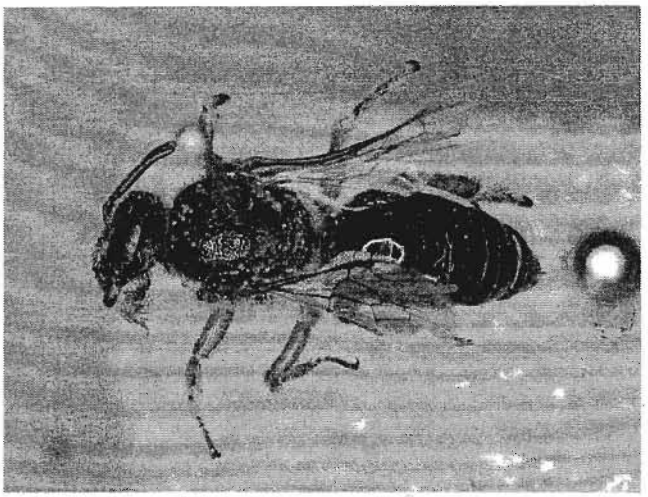


Fig. 77. Dorsal view of *Ctenoplectrina ugandica* (Cockerell) holotype.

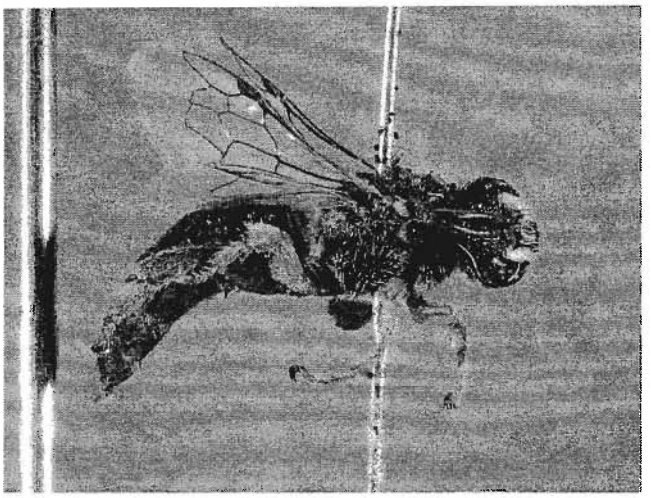
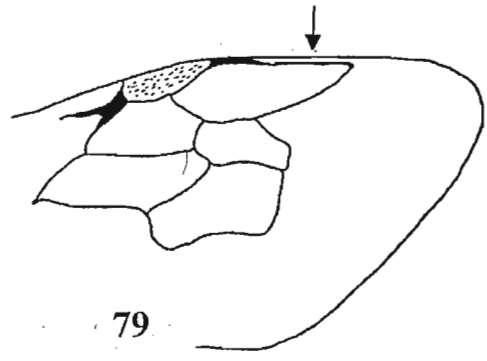


Fig. 78. Lateral view of *Ctenoplectrina ugandica* (Cockerell) holotype.



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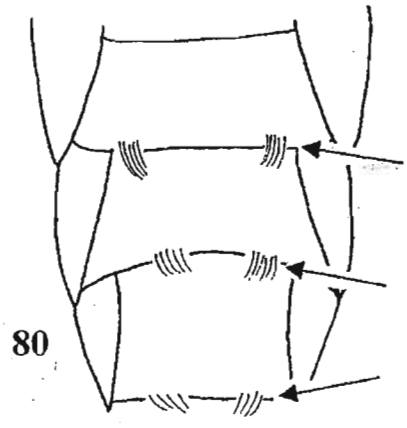

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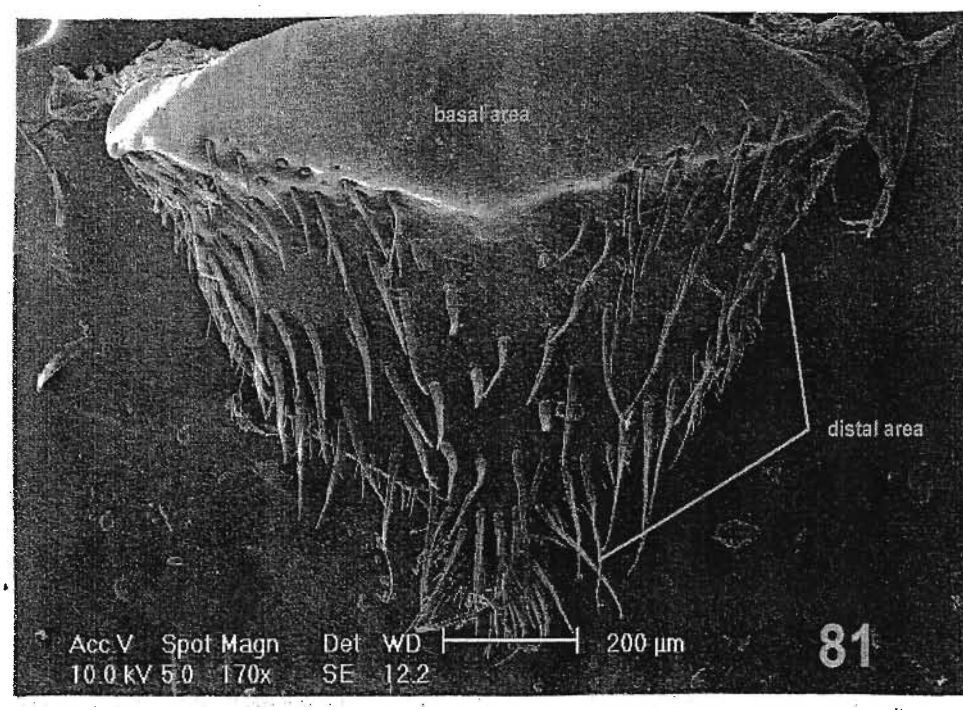
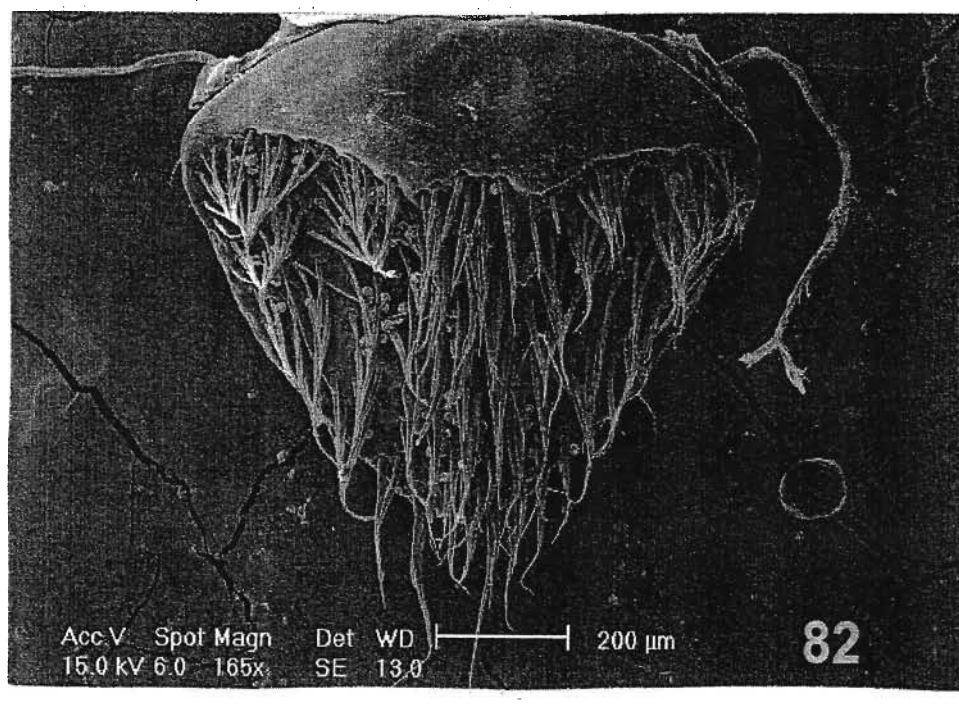
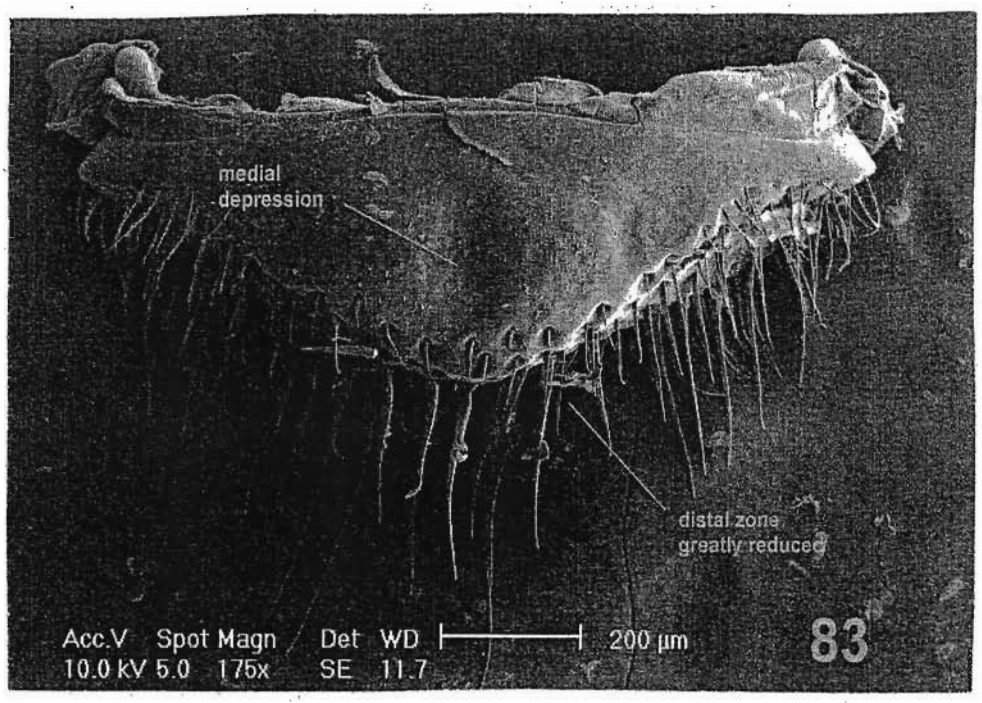
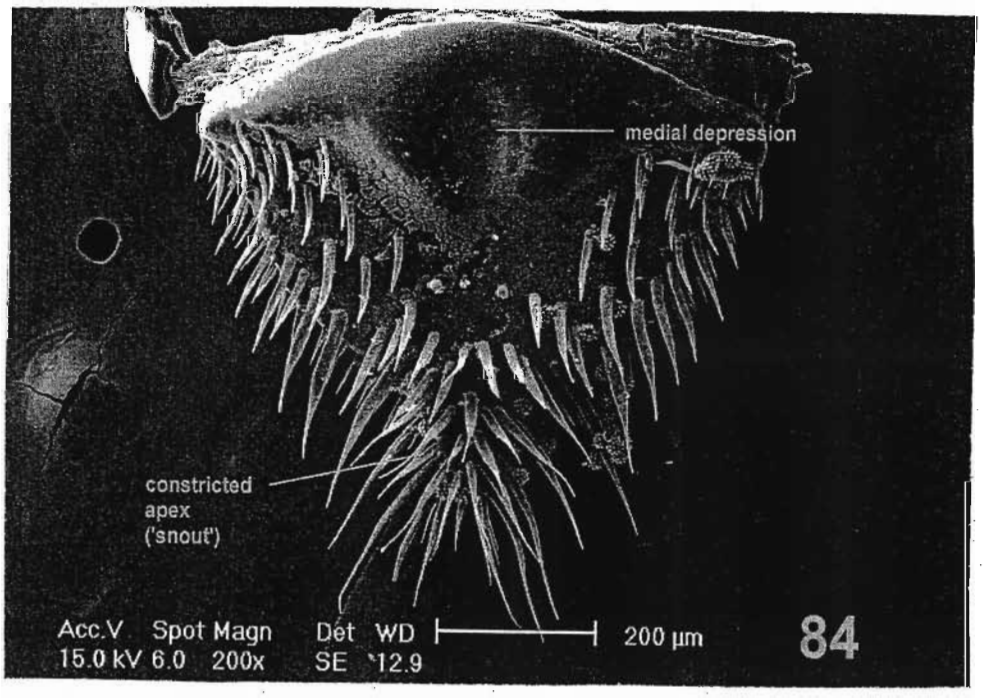
Figs. 79-80. *Ctenoplectrina ugandica* (Cockerell): (79) apical portion of forewing, (80) ventral view of metasomal sterna.



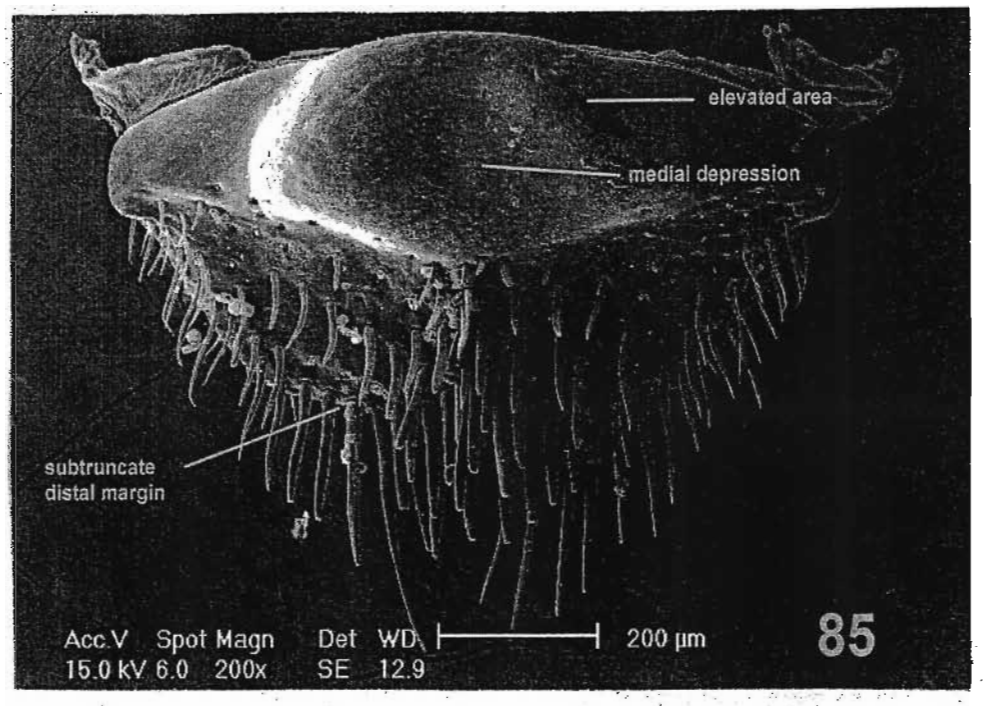


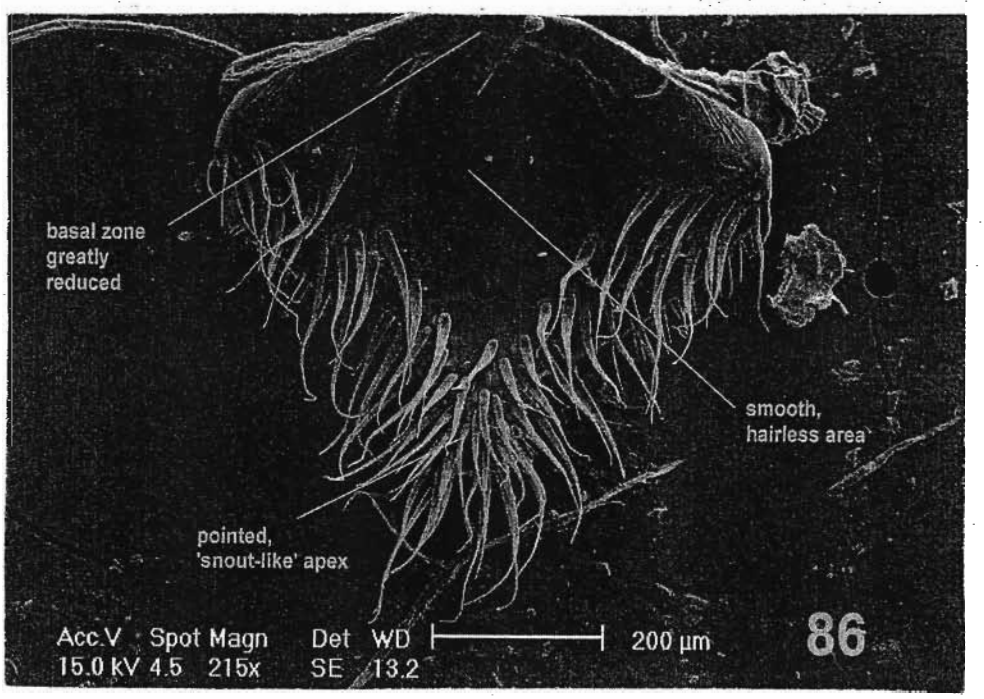
Figs 81-82. (81) Labrum of female *Scrapter heterodoxus* (Cockerell), (82) Labrum of female *Scrapter amplispinatus* Eardley.



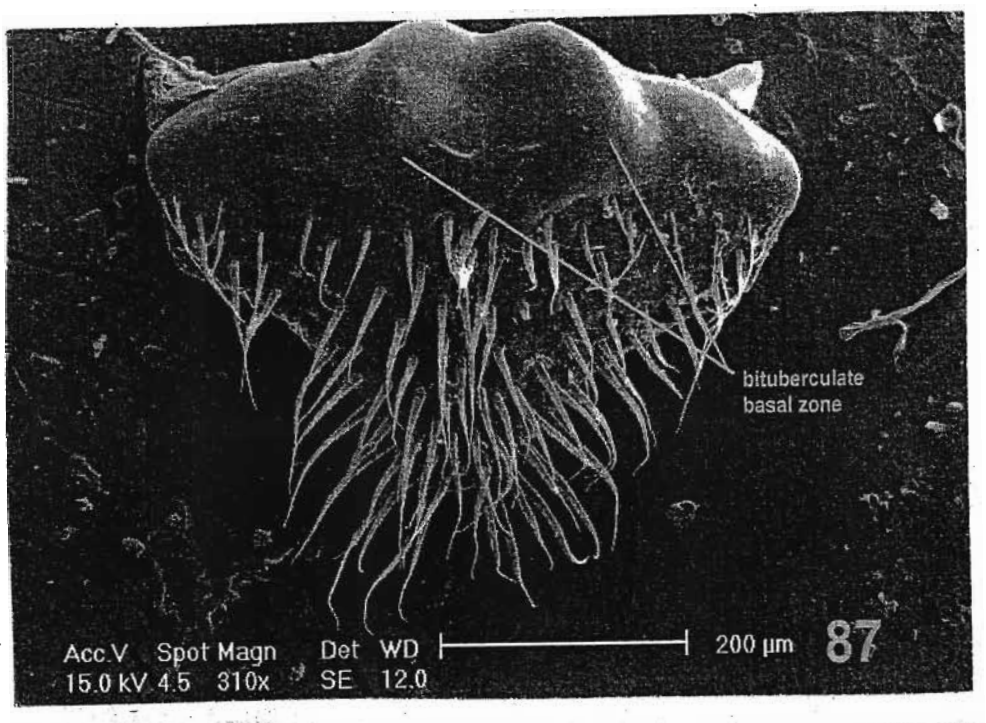


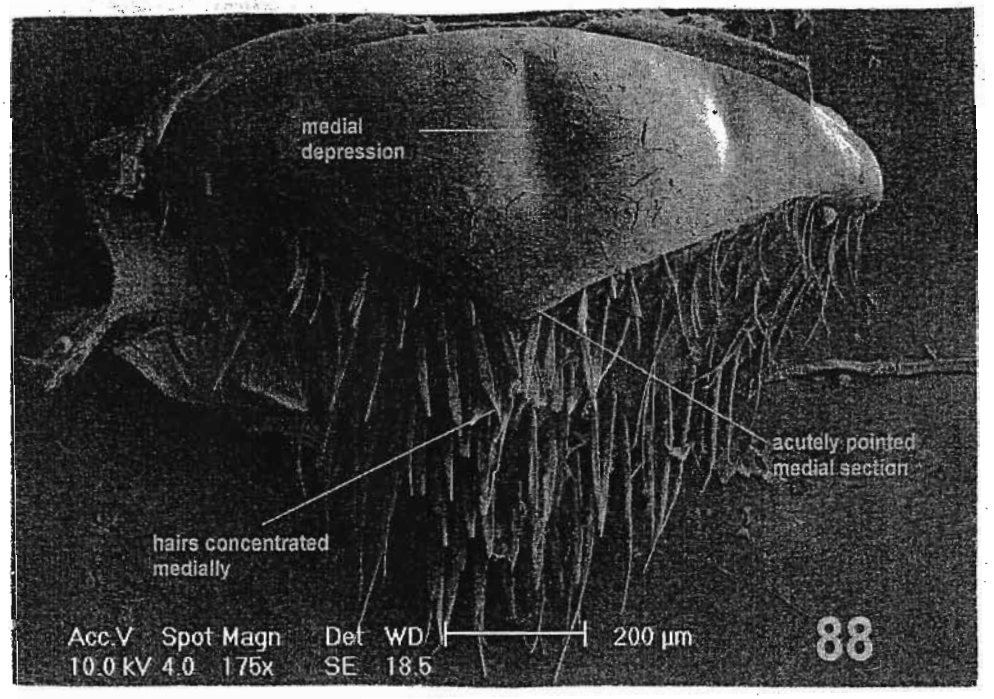
Figs 83-84. (83) Labrum of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (84) Labrum of female *Scrapter ruficornis* (Cockerell).



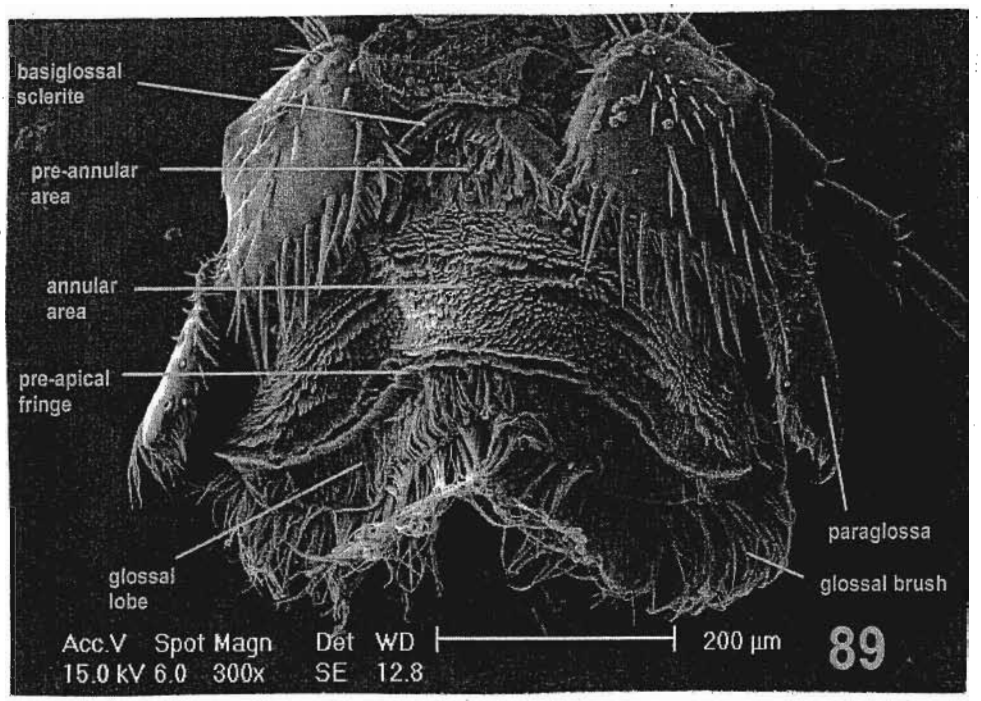


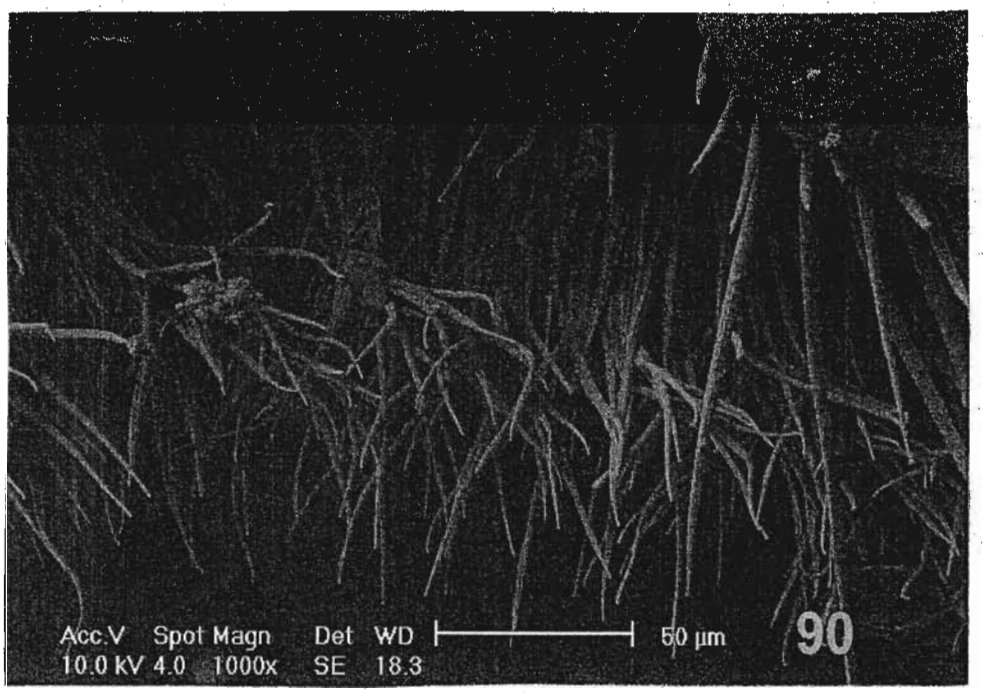
Figs 85-86. (85) Labrum of female *Scrapter algoensis* (Friese), (86) Labrum of female *Scrapter flavipes* (Friese).



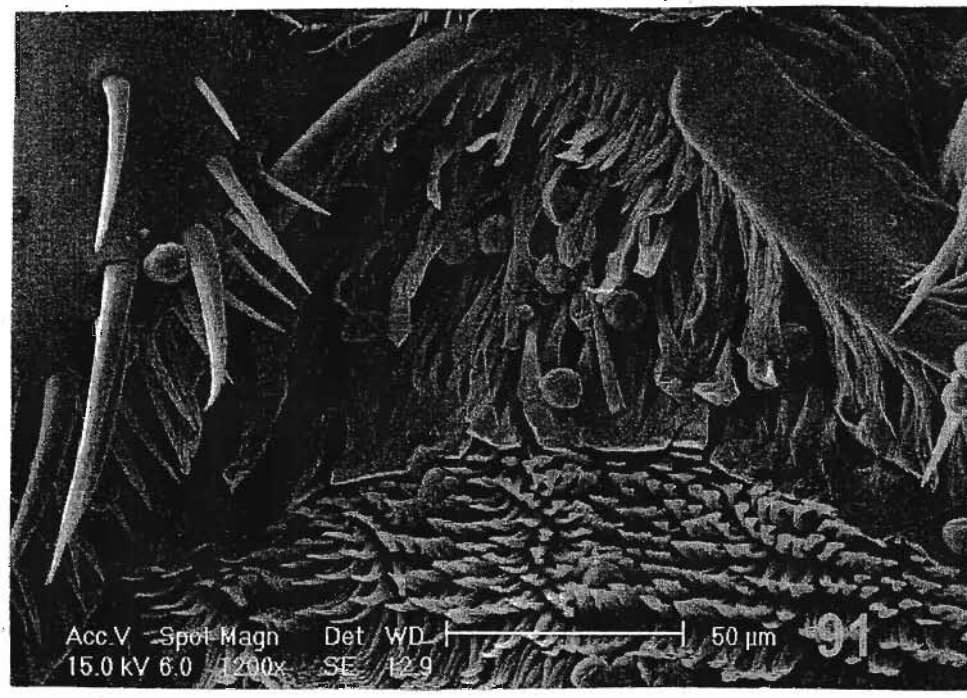


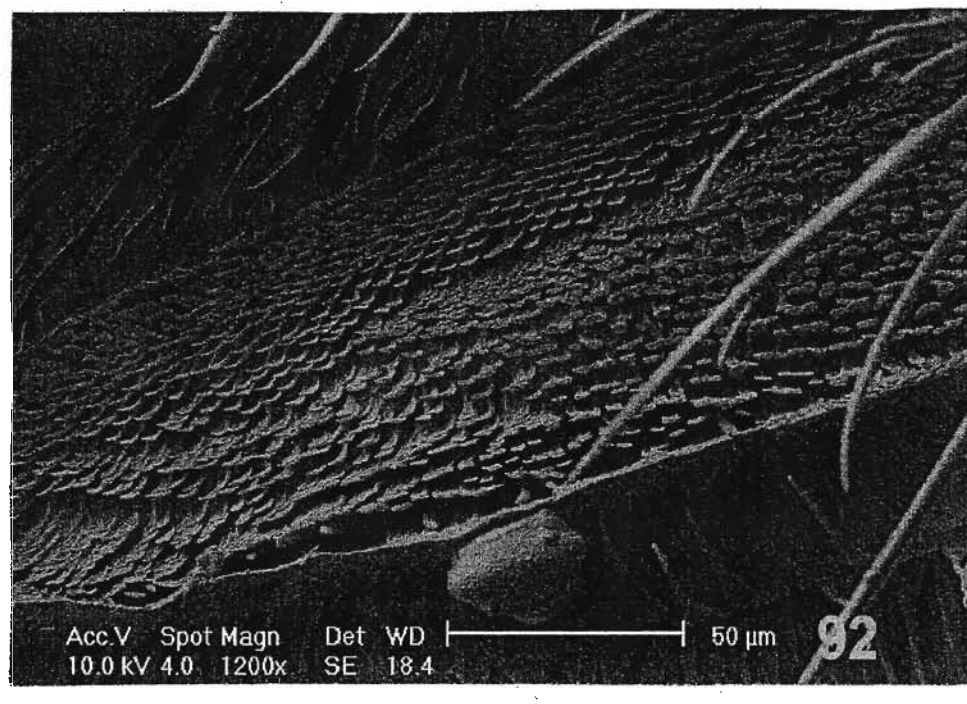
Figs 87-88. (87) Labrum of female *Scrapter albifumus* Eardley, (88) Labrum of female *Scrapter chloris* Eardley.



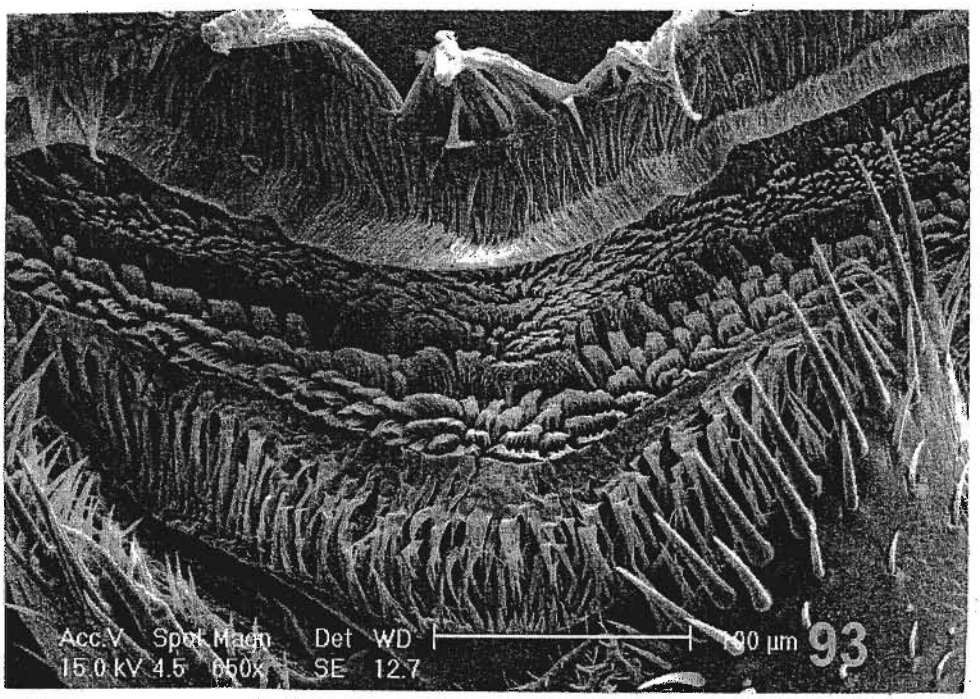


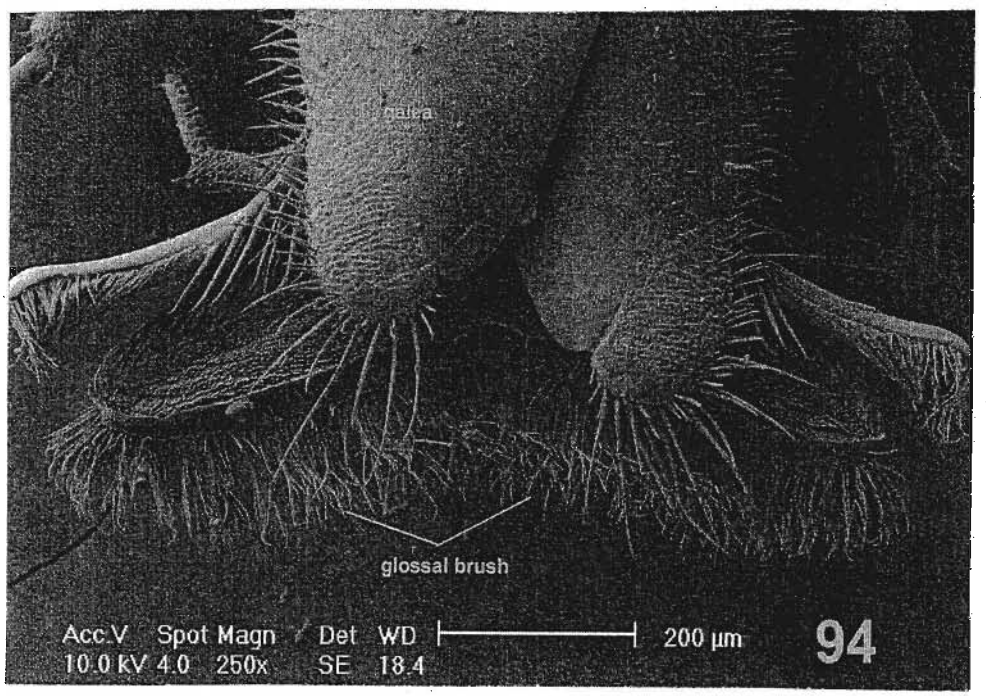
Figs 89-90. (89) Dorsal (anterior) view of female *Scrapter tomentum* Eardley glossa, (90) View of glossal brush of female *Scrapter chloris* Eardley.



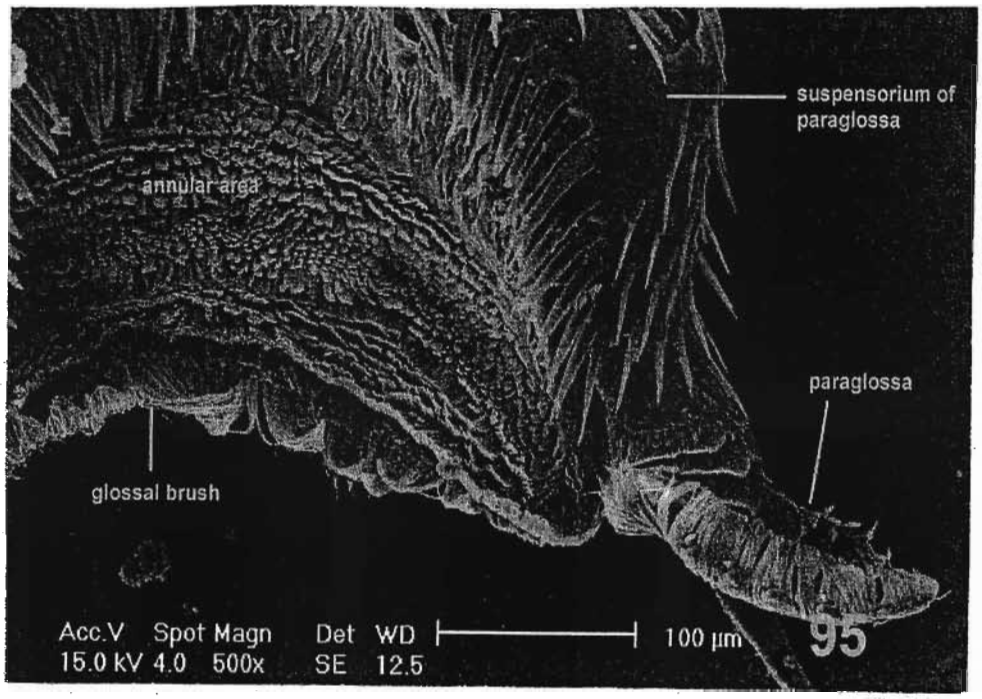


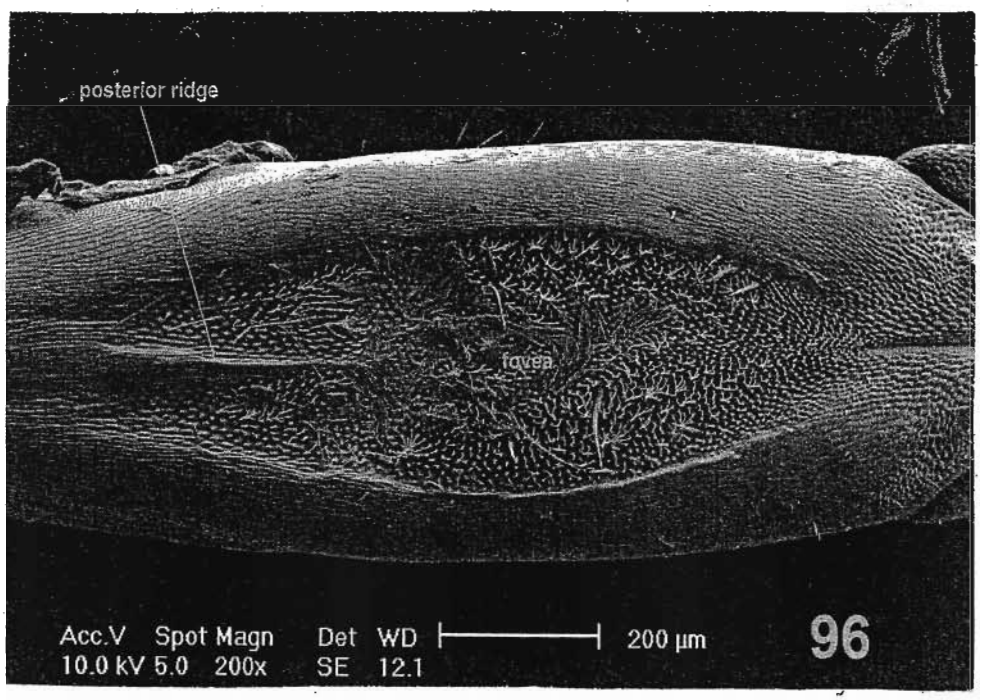
Figs 91-92. (91) Pre-annular area and basiglossal sclerite of female *Scrapter tomentum* Eardley, (92) Pre-apical fringe and annular area of female *Scrapter chloris* Eardley.





Figs 93-94. (93) Dorsal (anterior) view of female *Scrapter amplitarsus* (Friese) glossa, (94) Distal ends of galeae, glossa and paraglossae of female *Scrapter chloris* Eardley.





Figs 95-96. (95) Dorsal (anterior) view of euryglossine glossa and paraglossa, (96) Ventral view of prementum of female *Scrapter chloris* Eardley showing fovea.

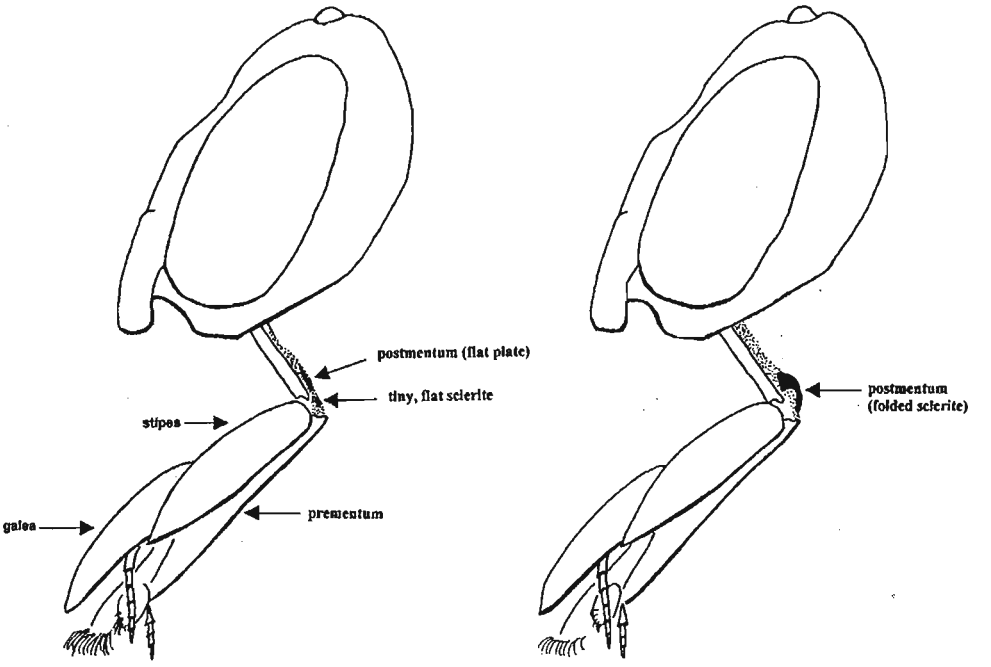
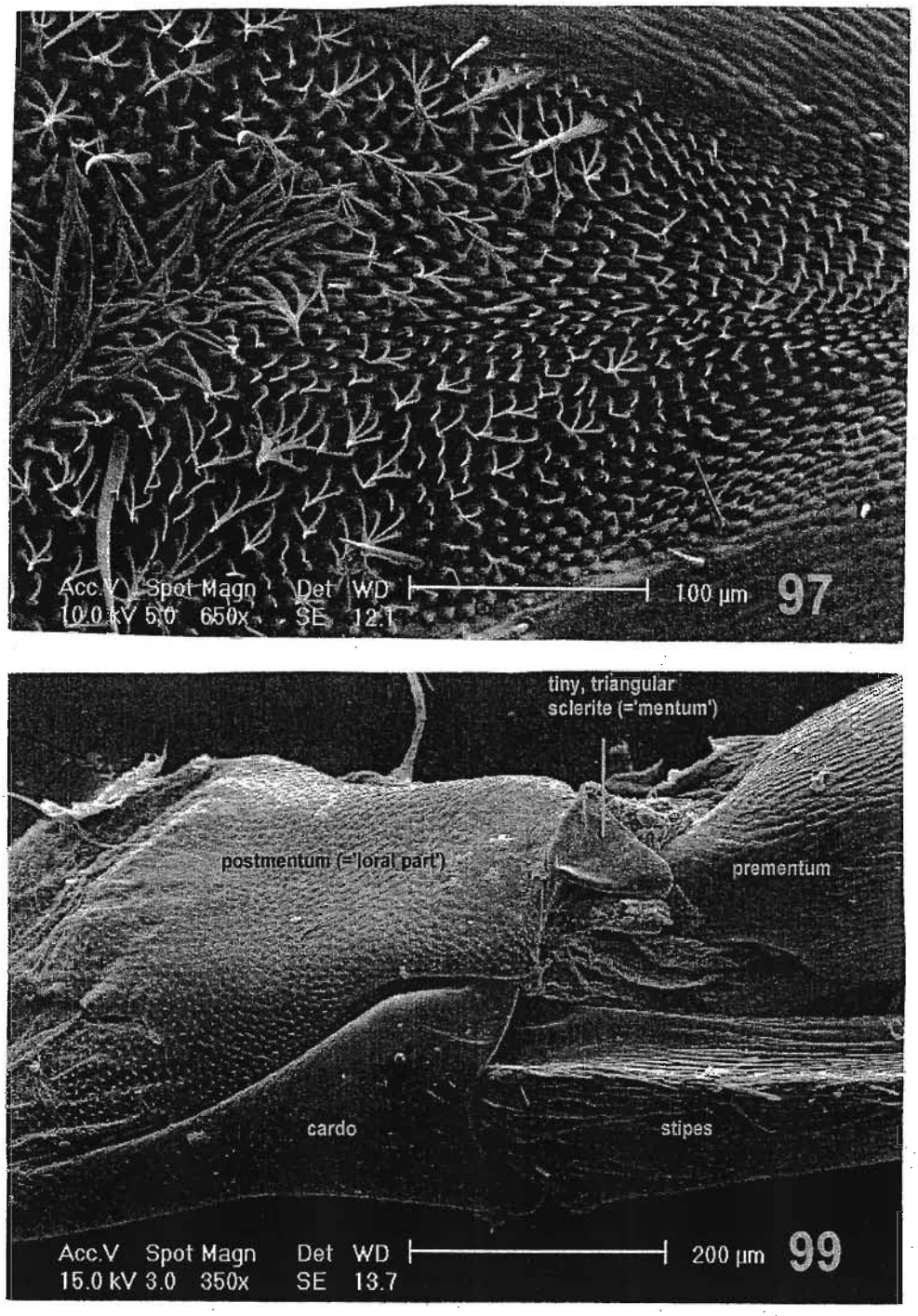
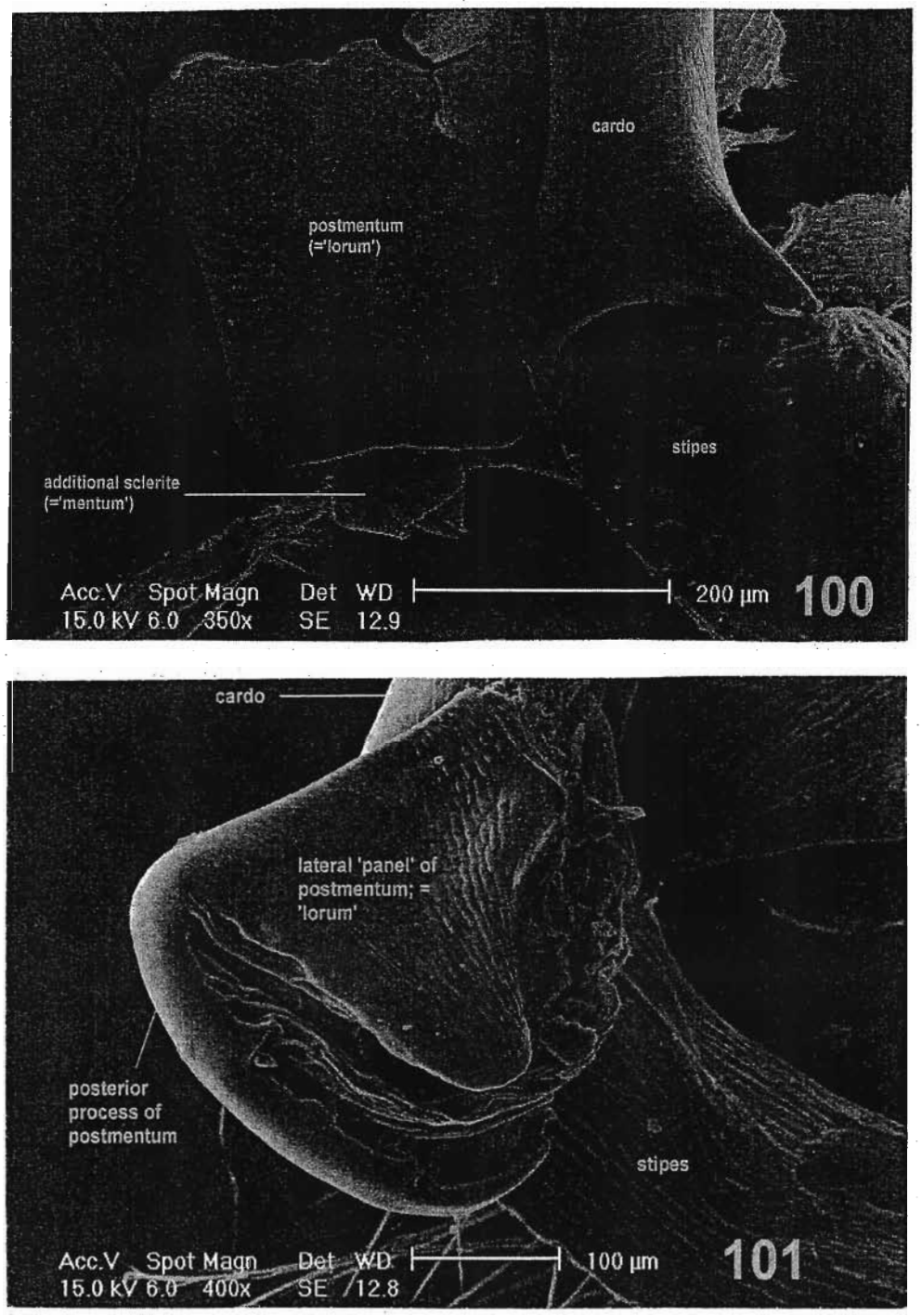


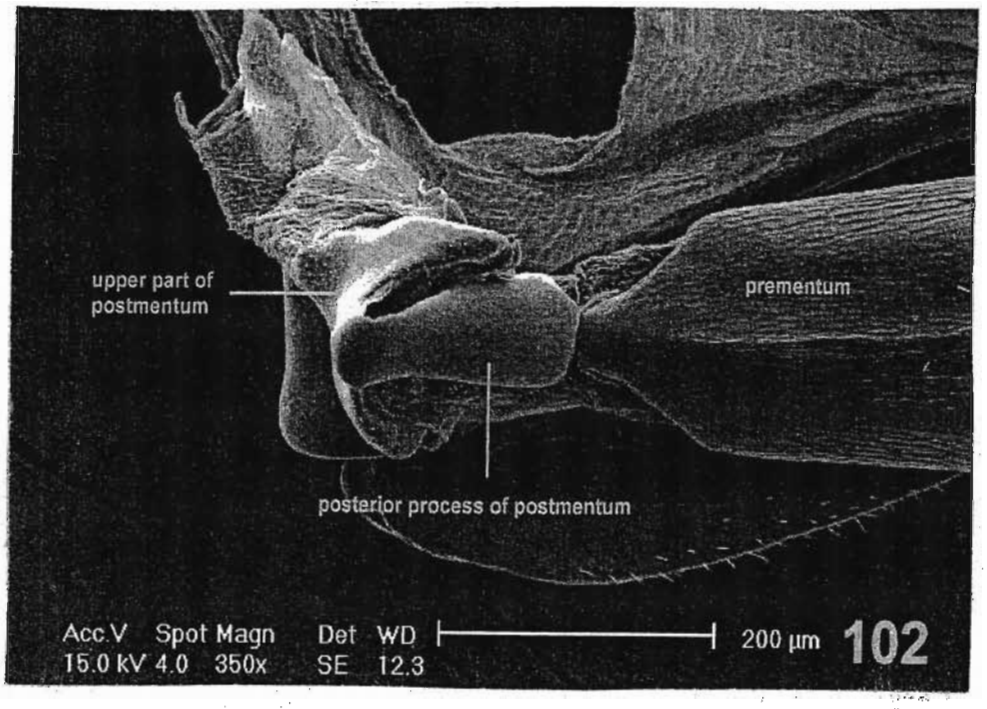
Fig. 98. Lateral view of mouthparts of *Scrapter* showing two postmentum configurations.

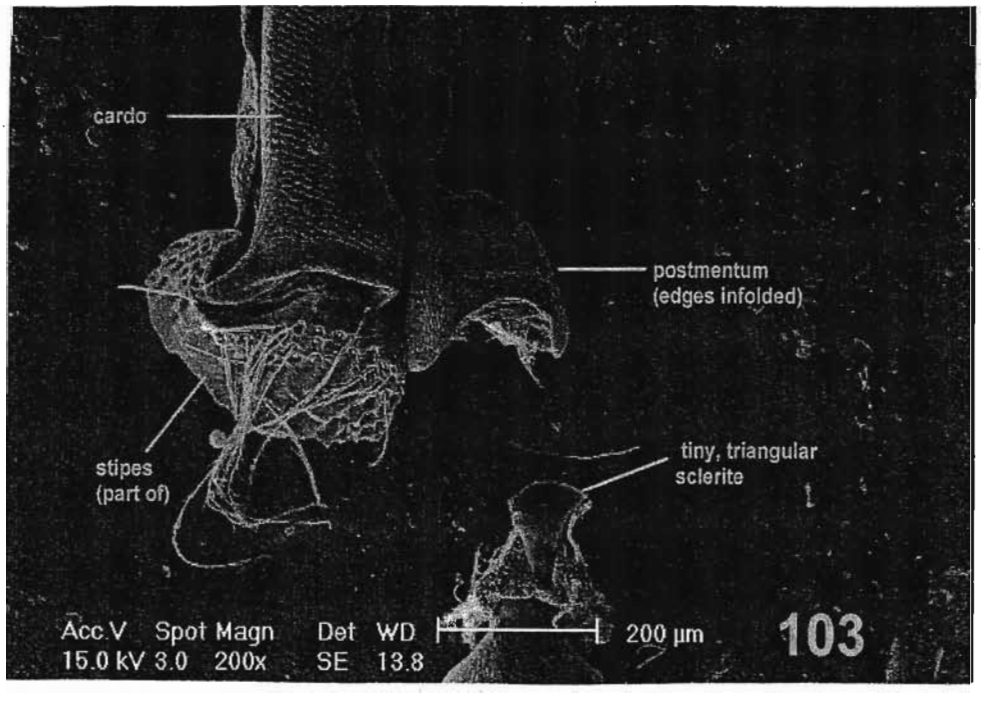


Figs 97, 99. (97) Spicules in premental fovea of female *Scrapter chloris* Eardley, (99) Posterior view of postmentum and associated features of female *Scrapter chloris* Eardley.

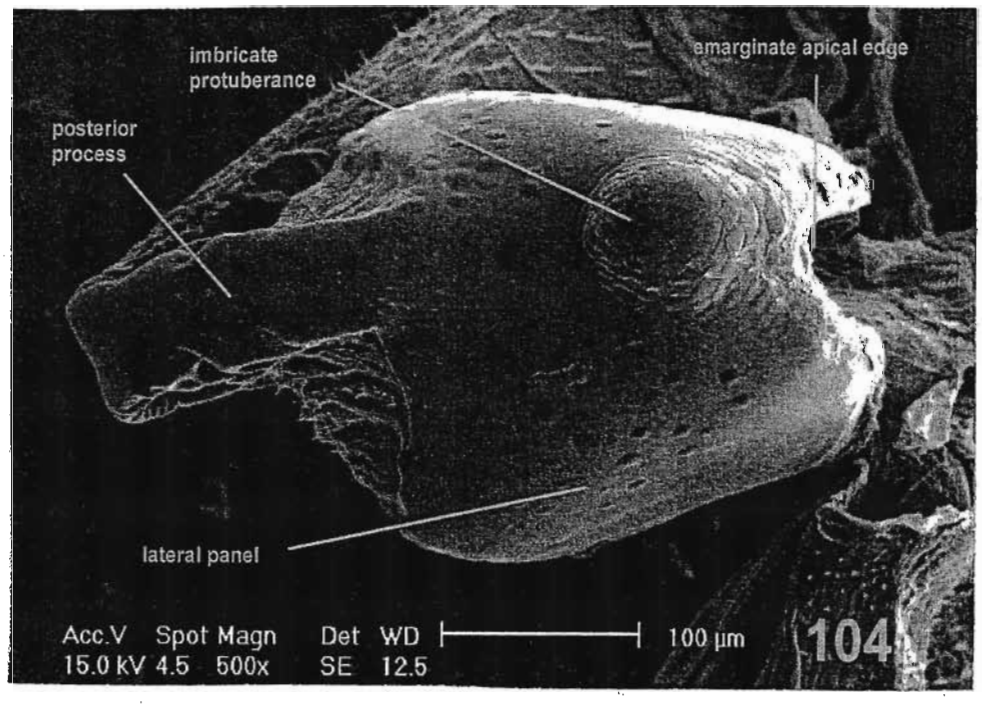


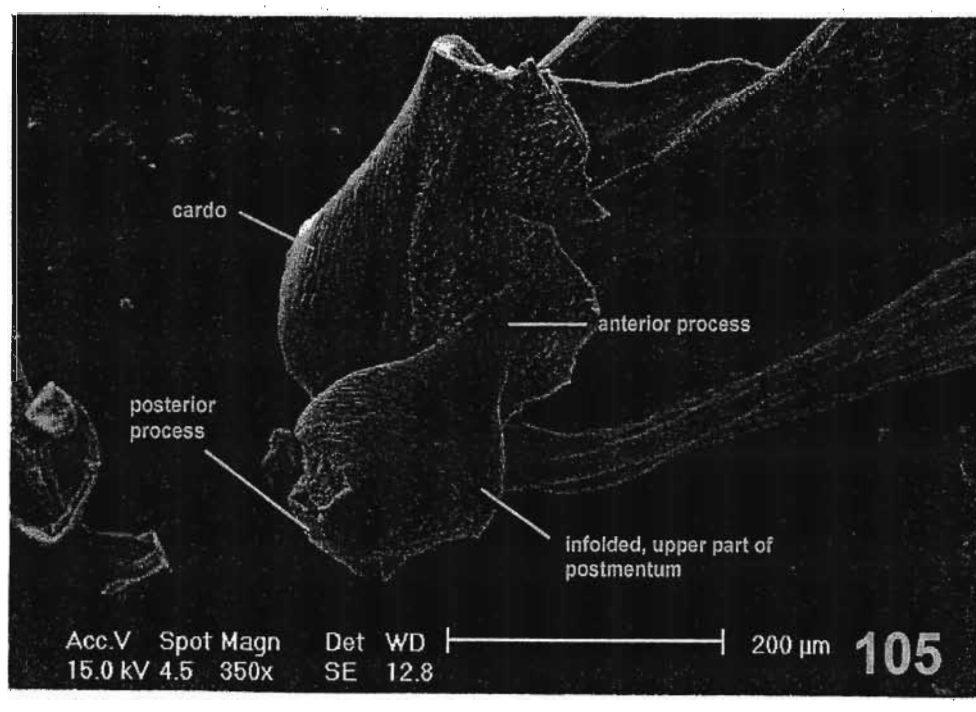
Figs 100-101. (100) Posterior view of postmentum and cardo of female *Scrapter algoensis* (Friese), (101) Lateral view of postmentum of female *Scrapter amplispinatus* Eardley.



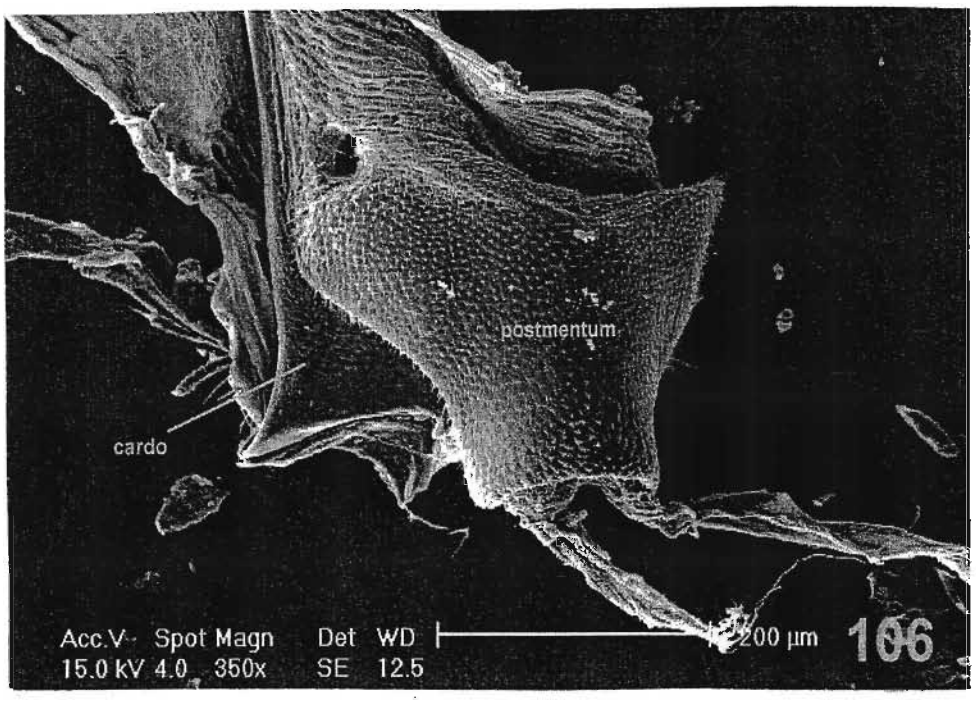


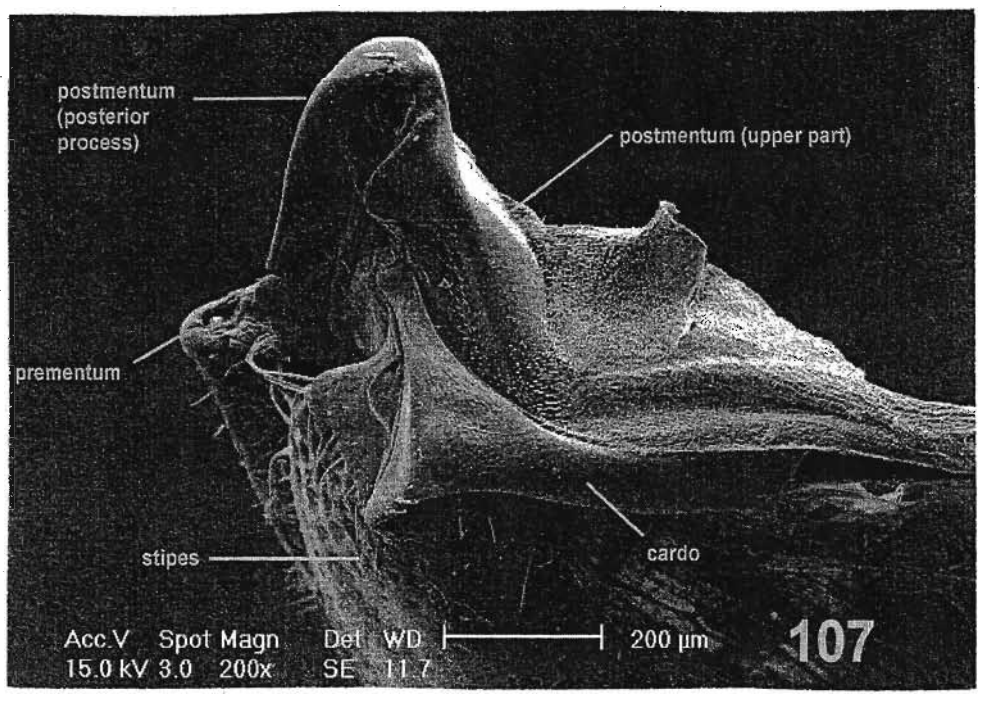
Figs 102-103. (102) Oblique posterior view of postmentum and associated structures of female *Scrapter nitidus* (Friese), (103) Posterior view of postmentum and associated structures of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville.



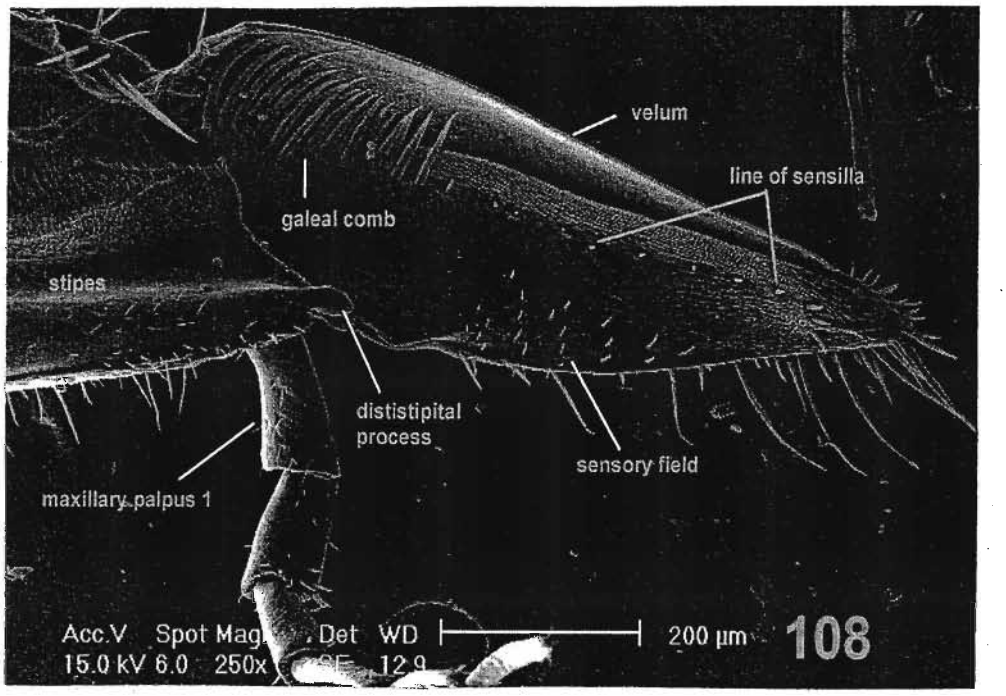


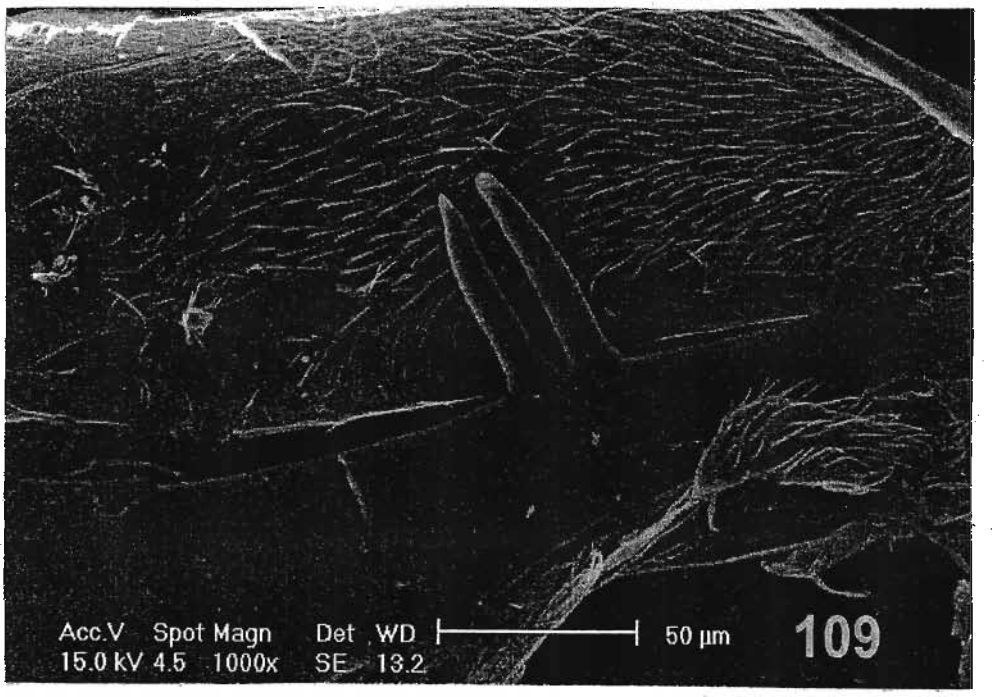
Figs 104-105. (104) Dorsal view of postmentum of female *Scrapter heterodoxus* (Cockerell), (105) Oblique dorsal view of postmentum of female *Scrapter caesariatus* Eardley.



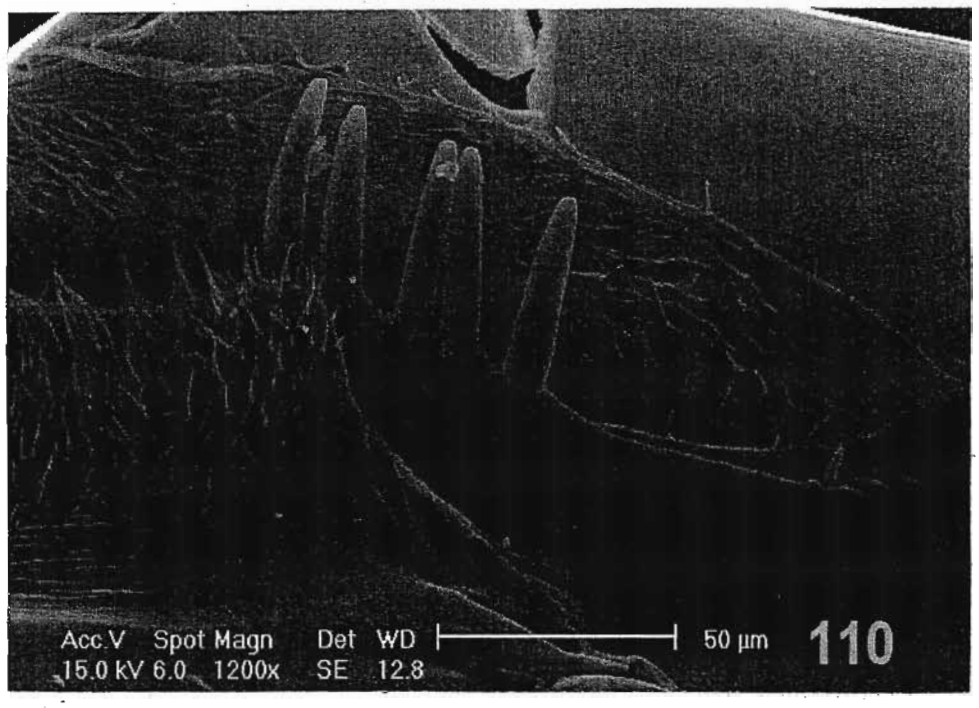


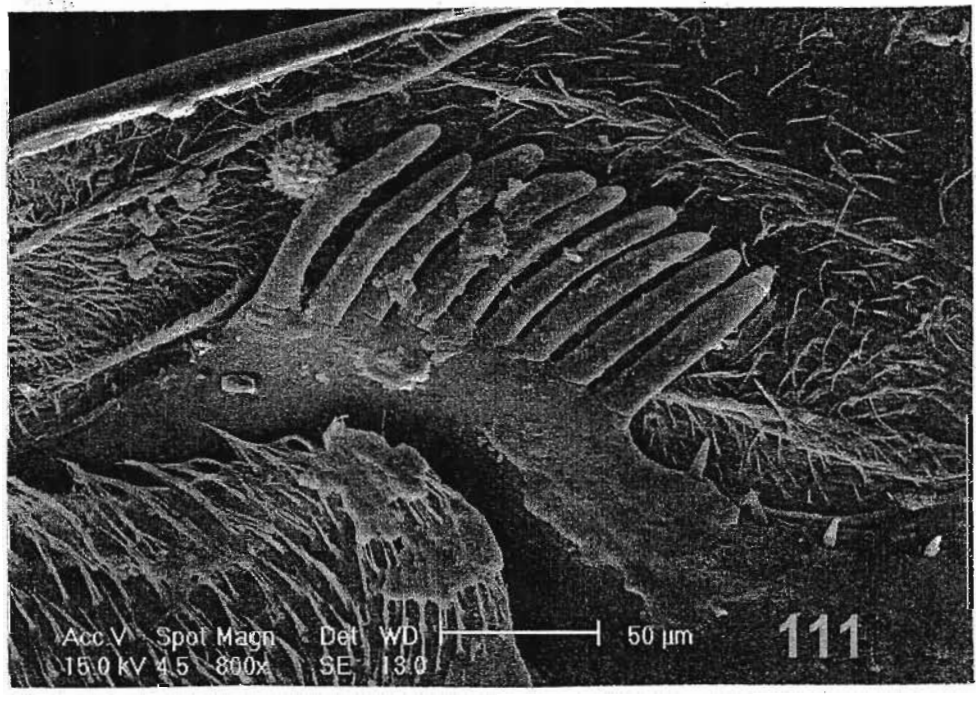
Figs 106-107. (106) Posterior view of postmentum of euryglossine bee, (107) Lateral view of postmentum of *Paracolletes* species.



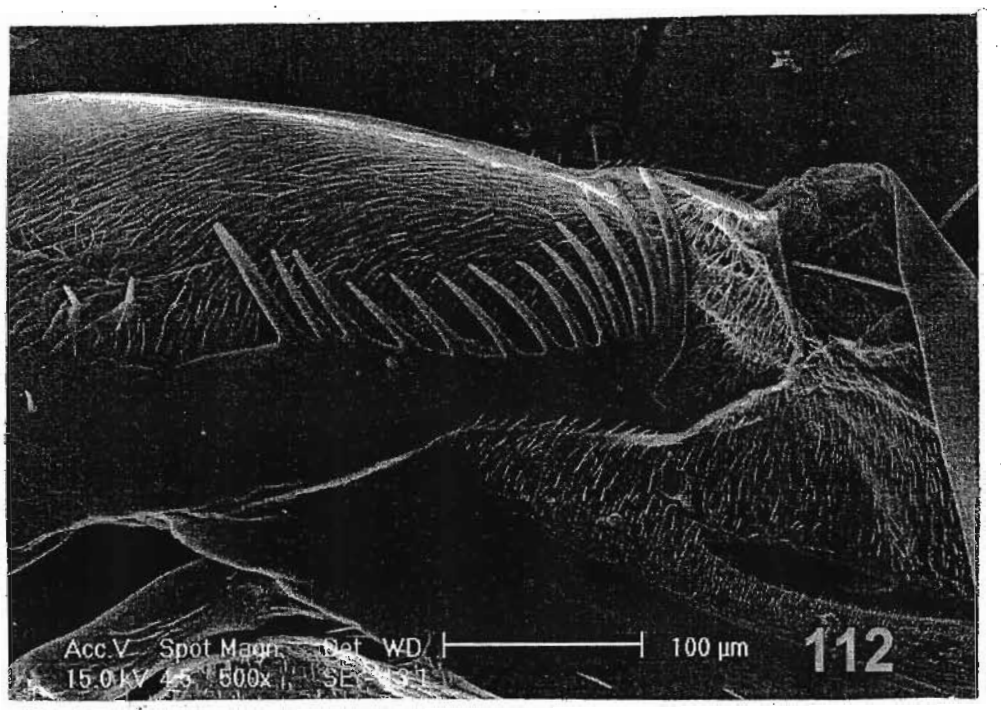


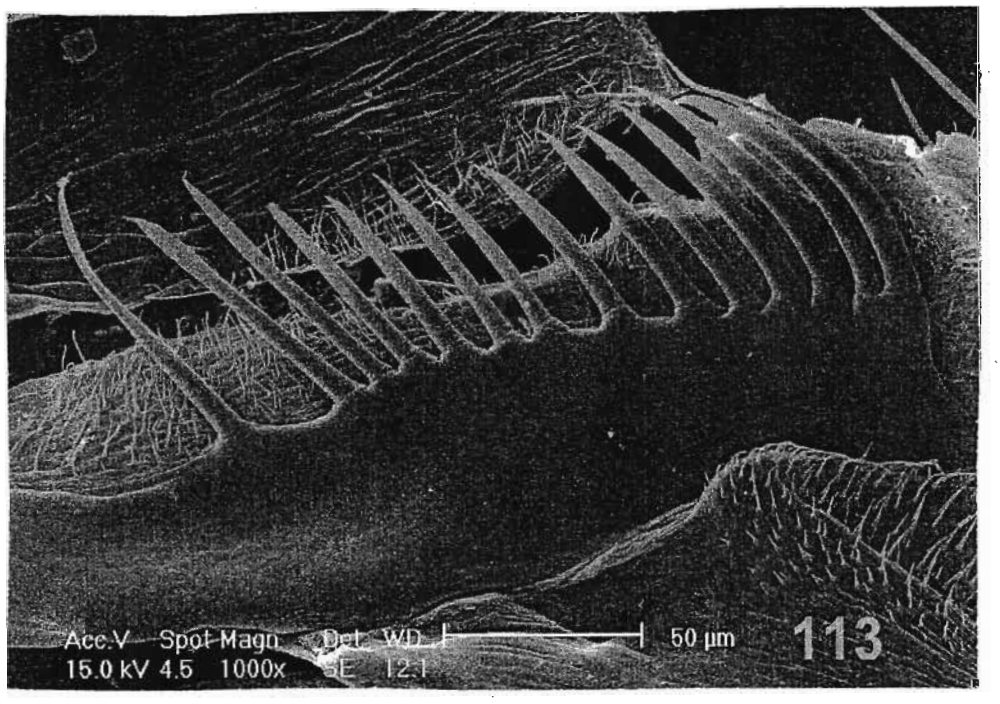
Figs 108-109. (108) Inner view of galea of female *Scrapter tomentum* Eardley, (109) Galeal comb of *Scrapter nitidus* (Friese).



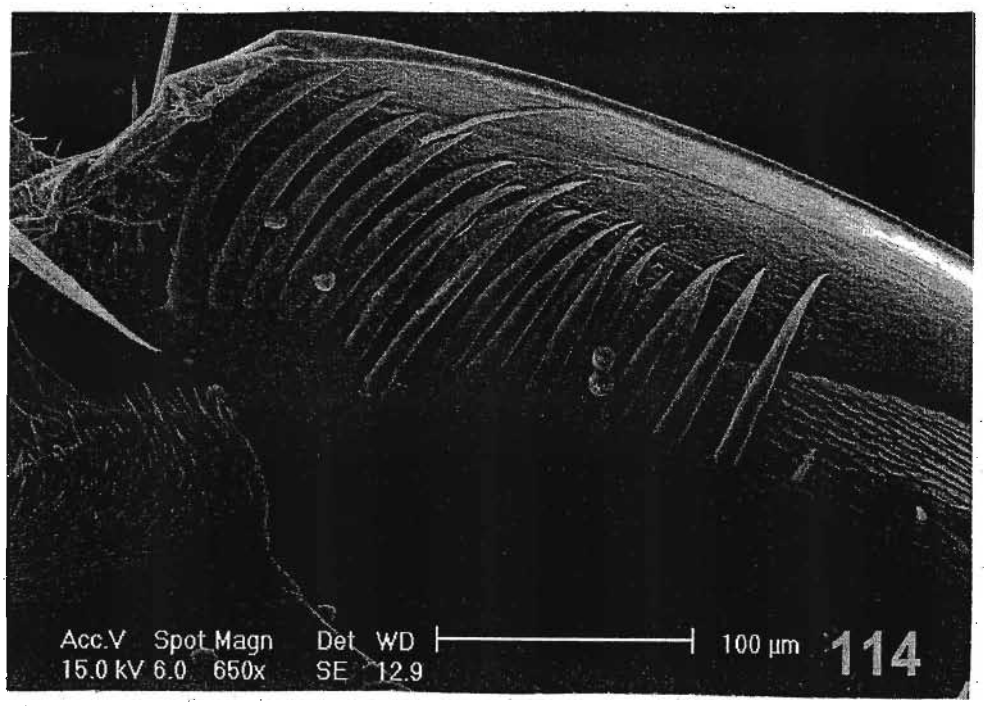


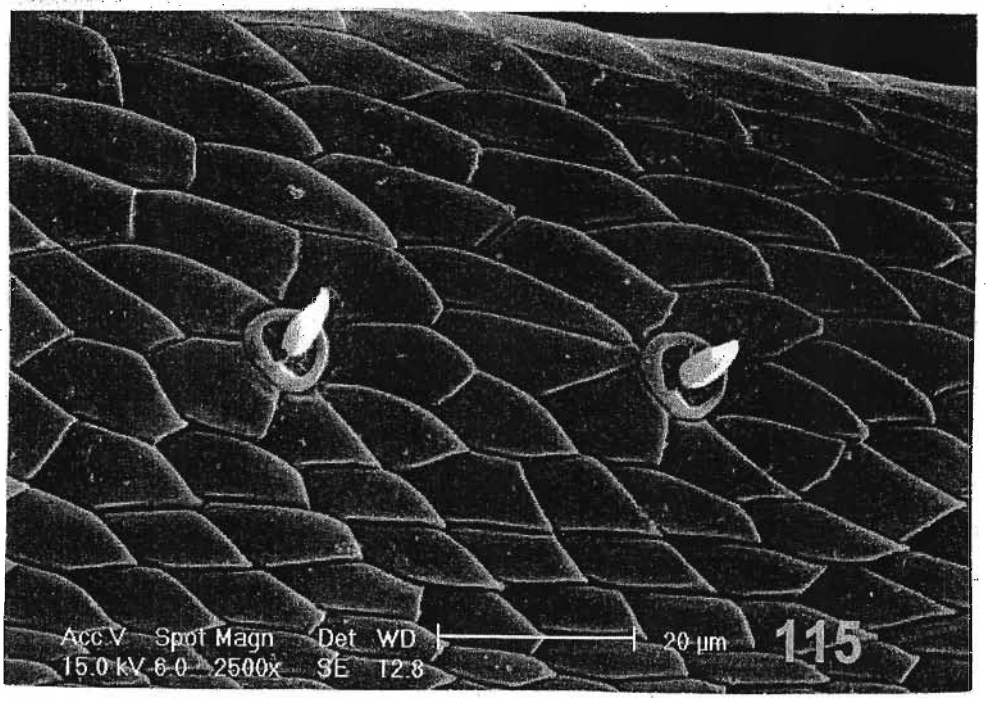
Figs 110-111. (110) Galeal comb of *Scrapter aureiferus* Cockerell, (111) Galeal comb of *Scrapter heterodoxus* (Cockerell).



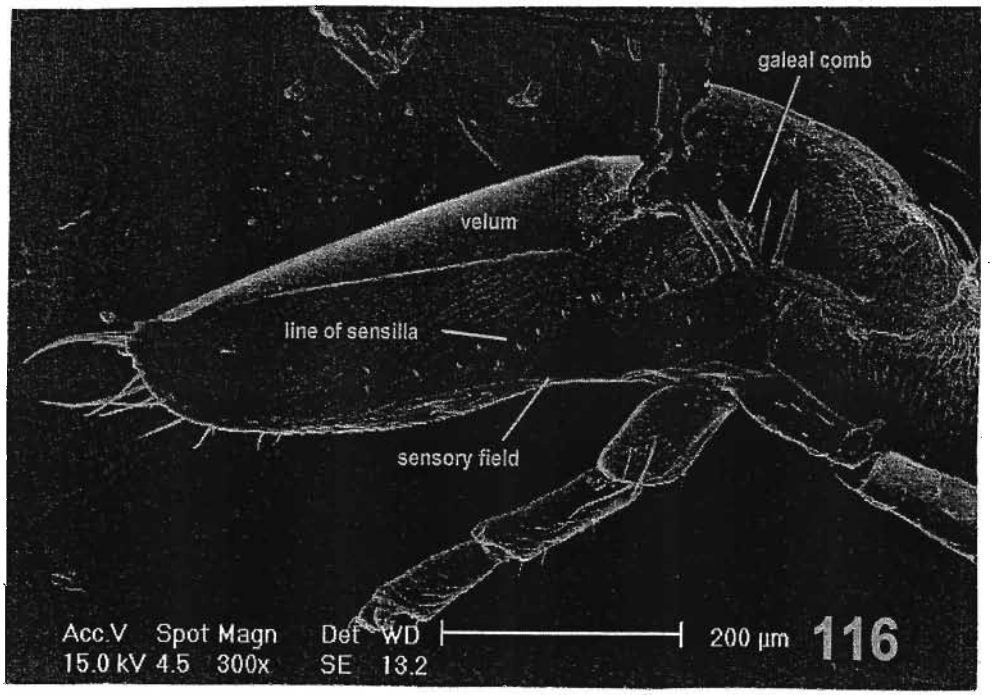


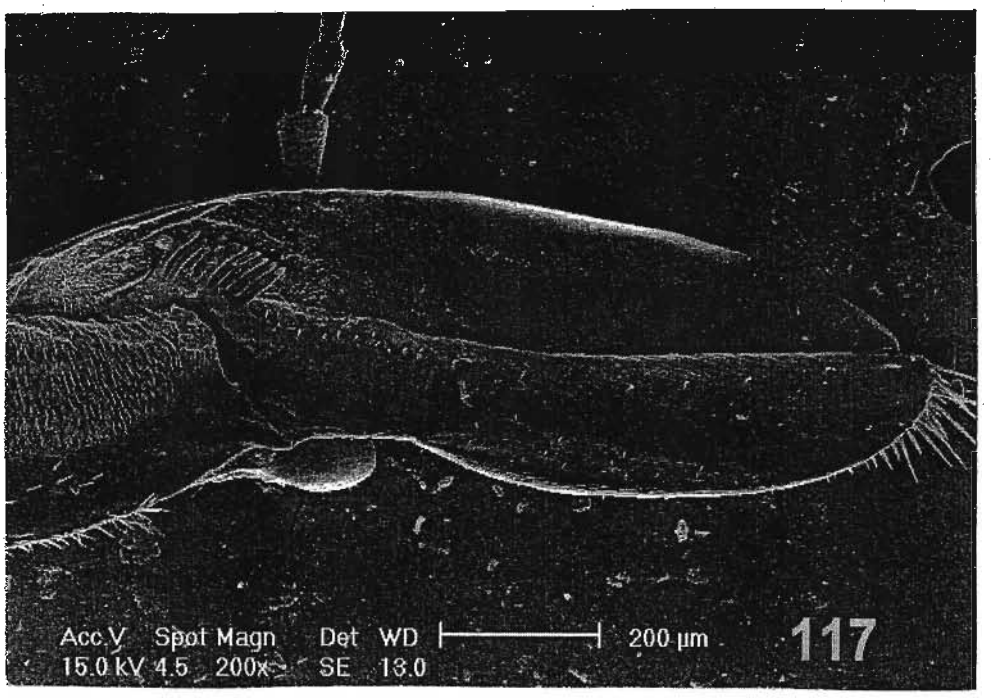
Figs 112-113. (112) Galeal comb of *Scrapter caesariatus* Eardley, (113) Galeal comb of *Scrapter albifumus* Eardley.



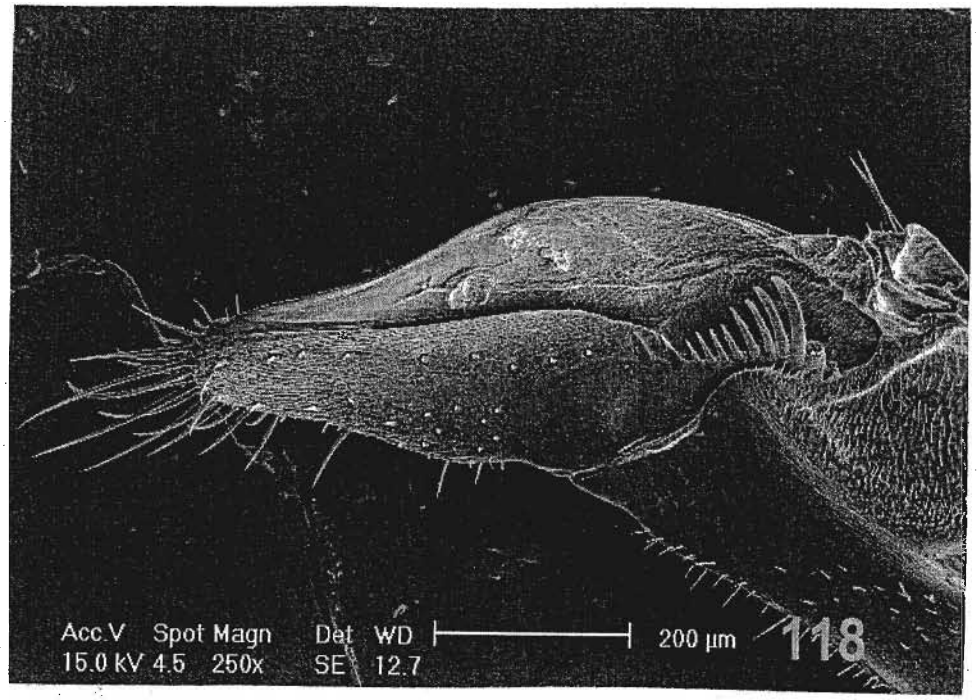


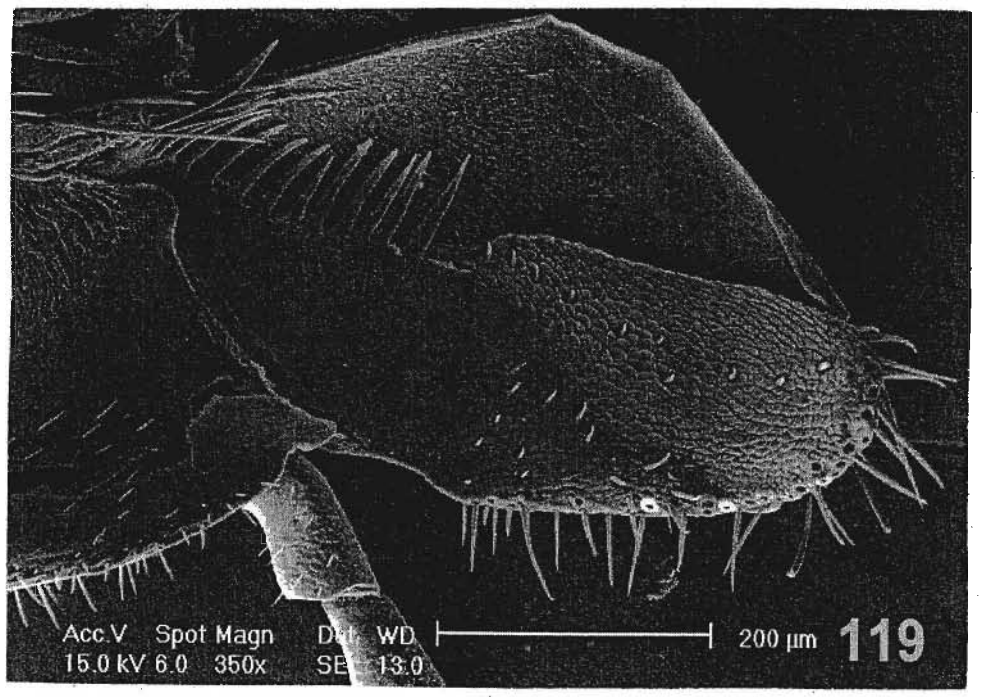
Figs 114-115. (114) Galeal comb of *Scrapter tomentum* Eardley, (115) Sensilla from sensillar line of galea in *Scrapter amplitarsus* (Friese).



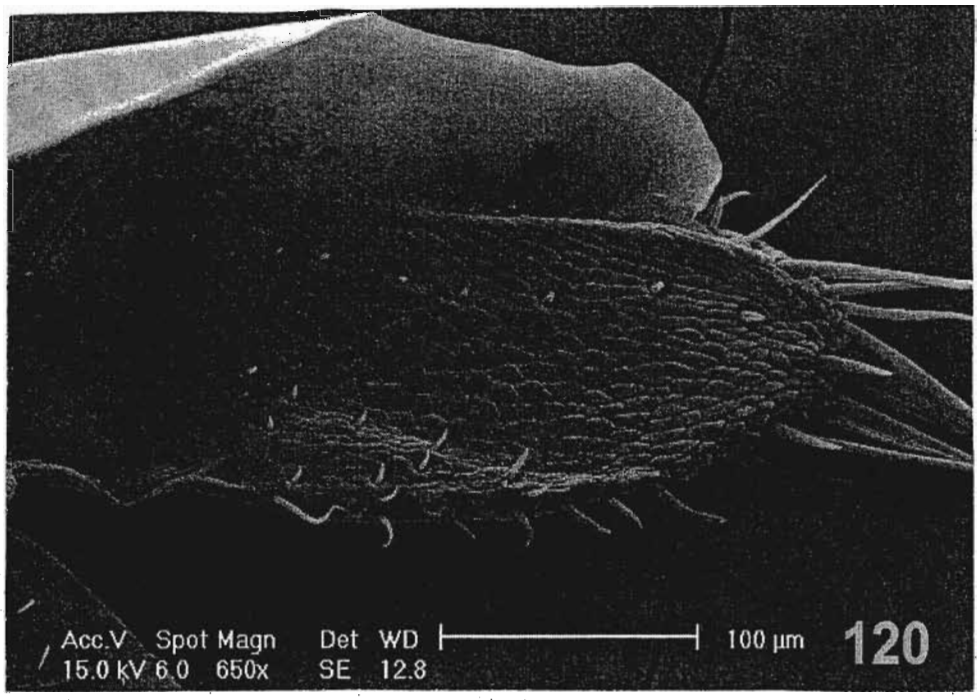


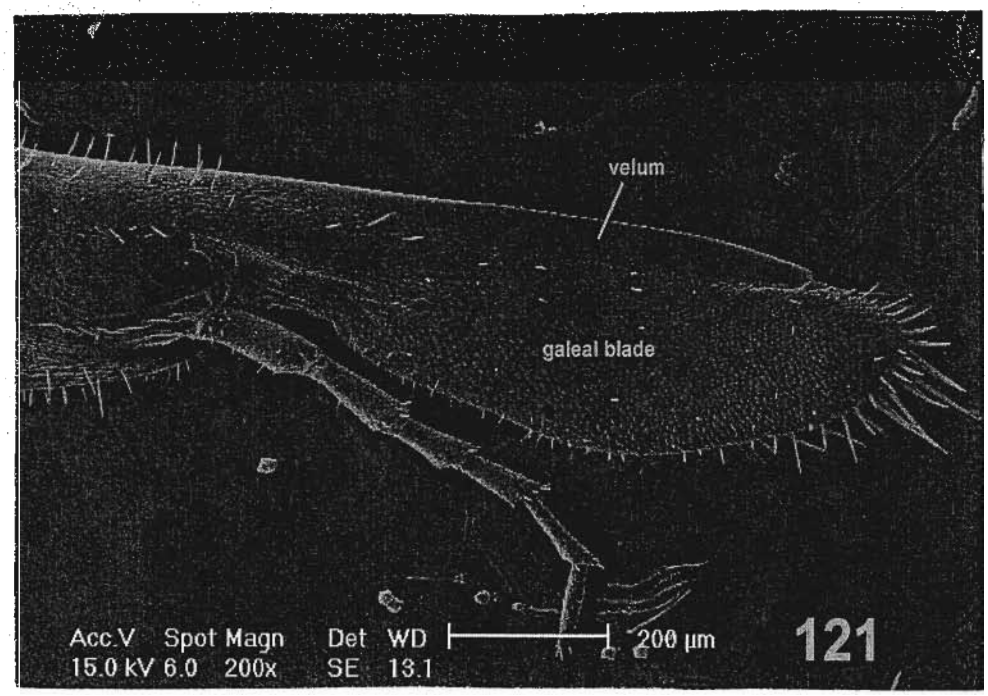
Figs 116-117. (116) Inner view of galea of female *Scrapter flavipes* (Friese), (117) Inner view of galea of female *Scrapter heterodoxus* (Cockerell).



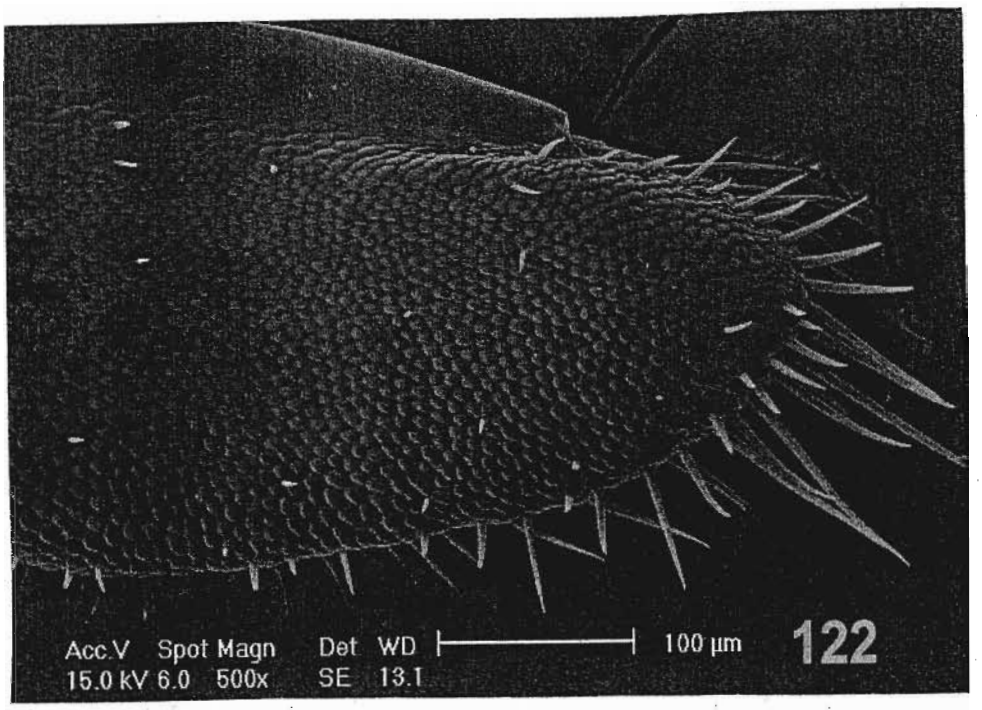


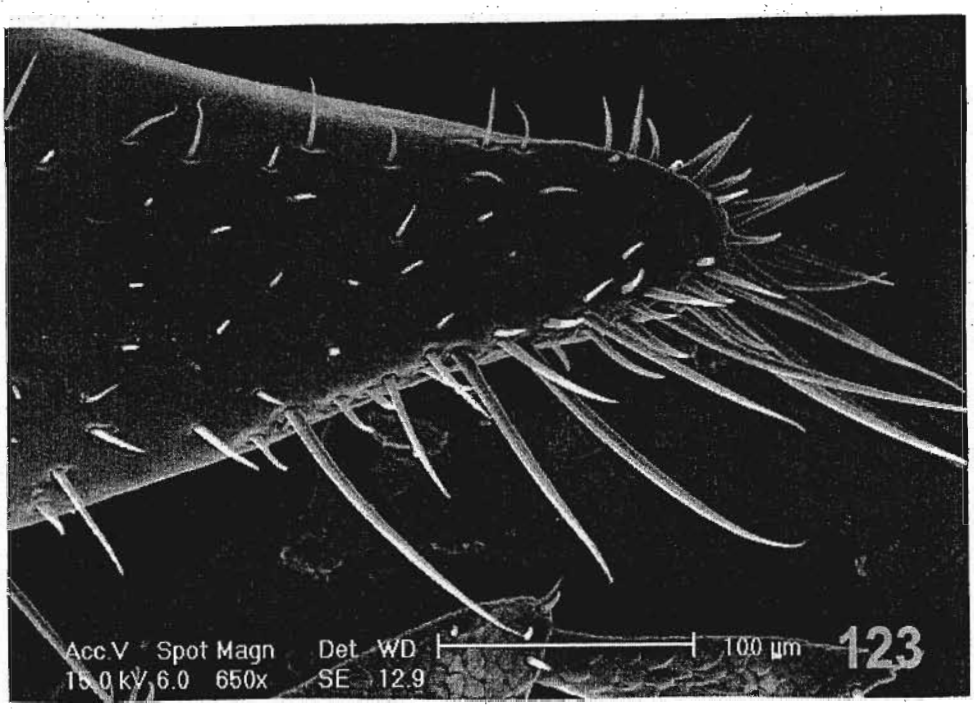
Figs 118-119. (118) Inner view of galea of female *Scrapter amplitarsus* (Friese), (119) Inner view of galea of female *Scrapter algoensis* (Friese).



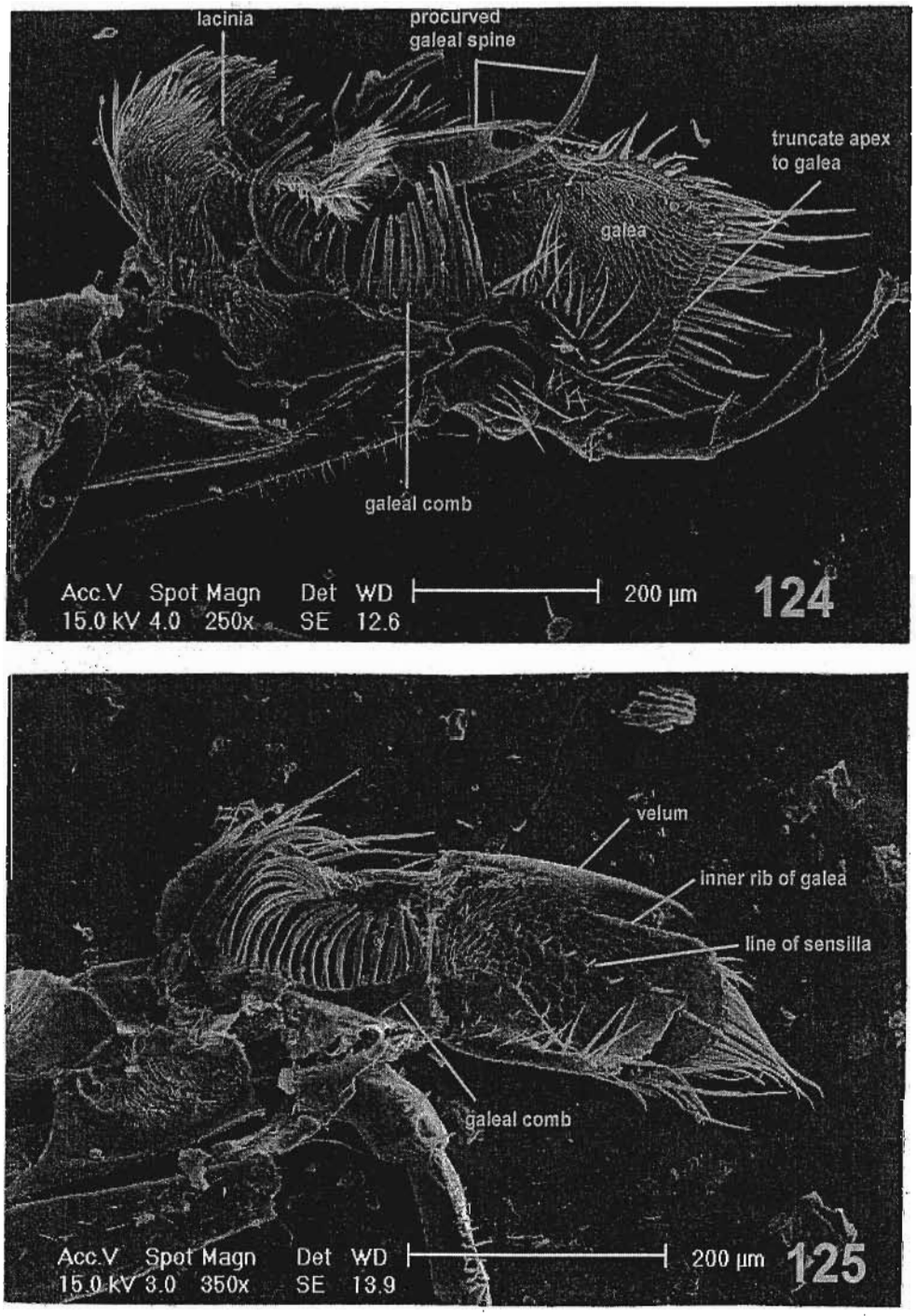


Figs 120-121. (120) Inner view of galea of female *Scrapter absonus* Eardley, (121) Outer view of galea and maxillary palp of female *Scrapter amplispinatus* Eardley.

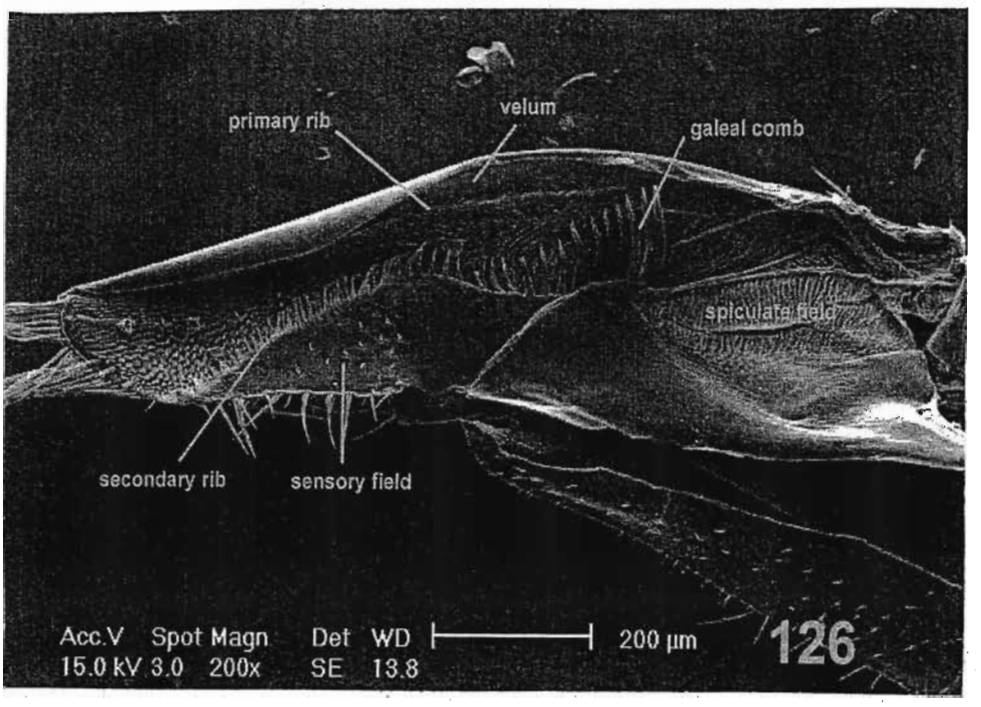


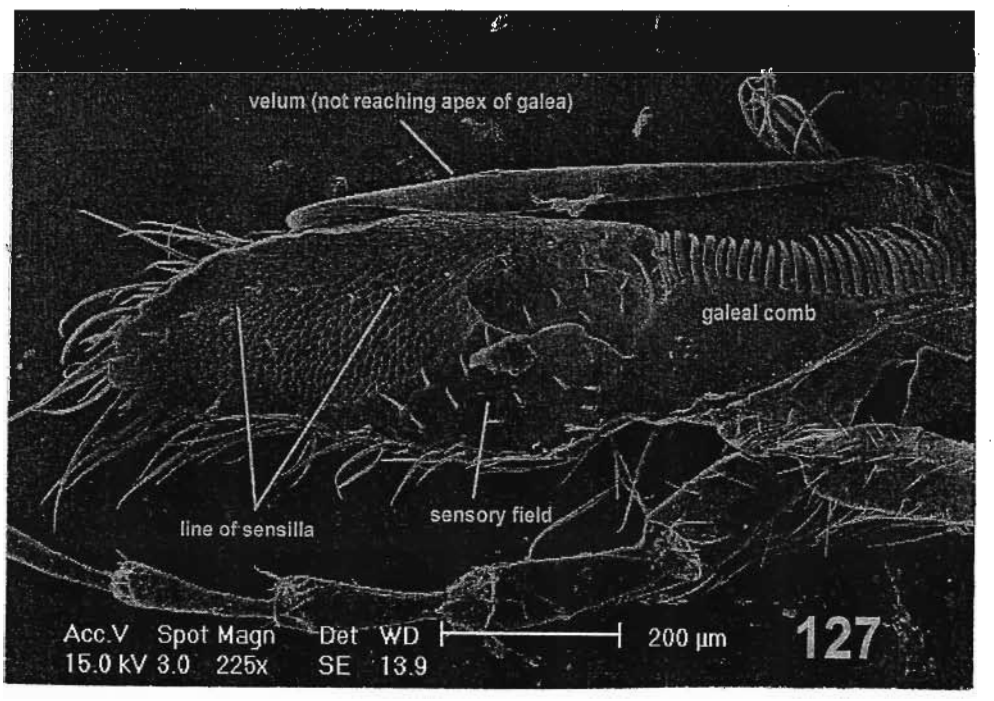


Figs 122-123. (122) Outer view of apex of galea of female *Scrapter amplispinatus* Eardley, (123) Outer view of apex of galea of female *Scrapter tomentum* Eardley.

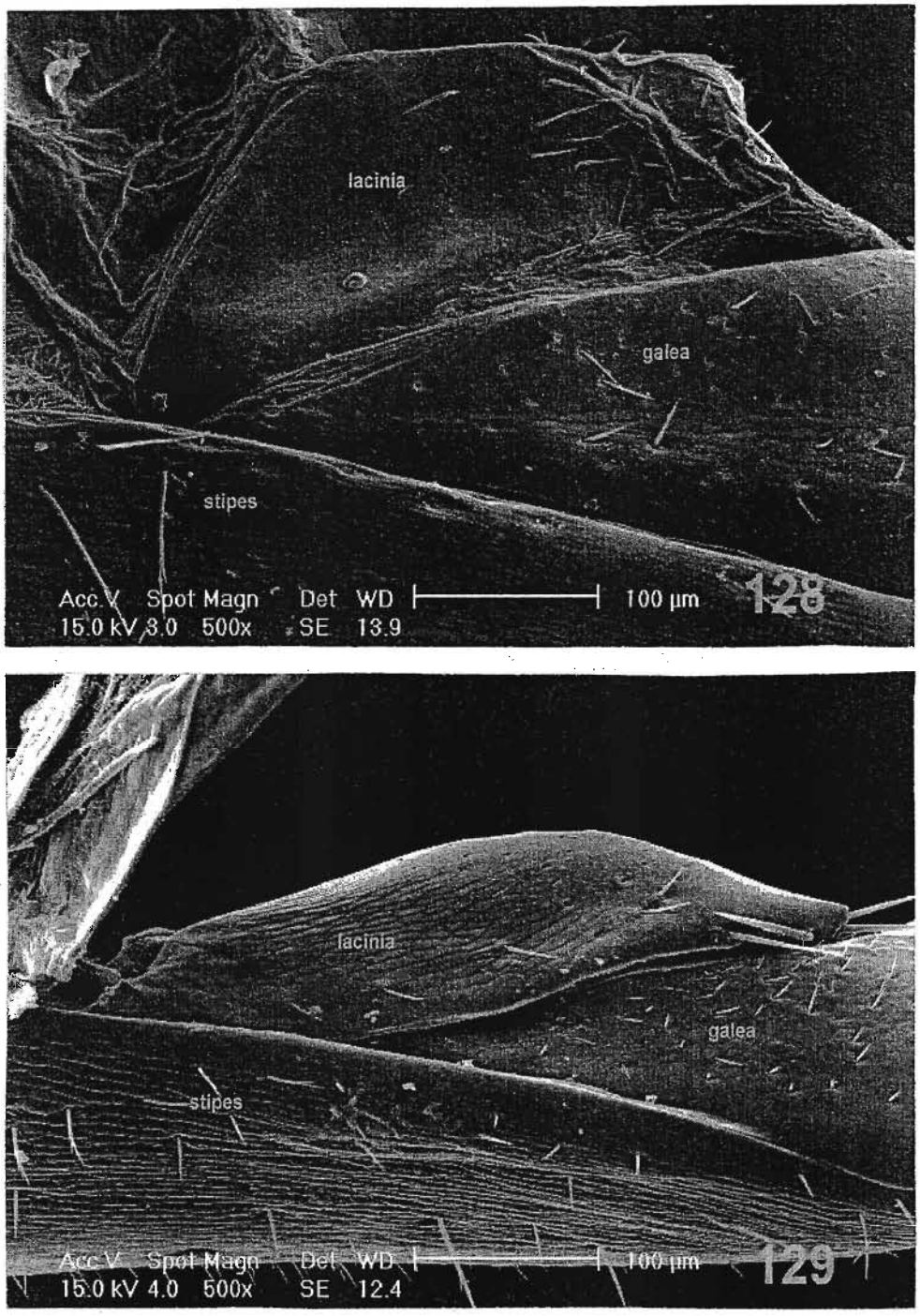


Figs 124-125. (124) Inner view of galea of euryglossine bee, (125) Inner view of galea of hylaeine bee.

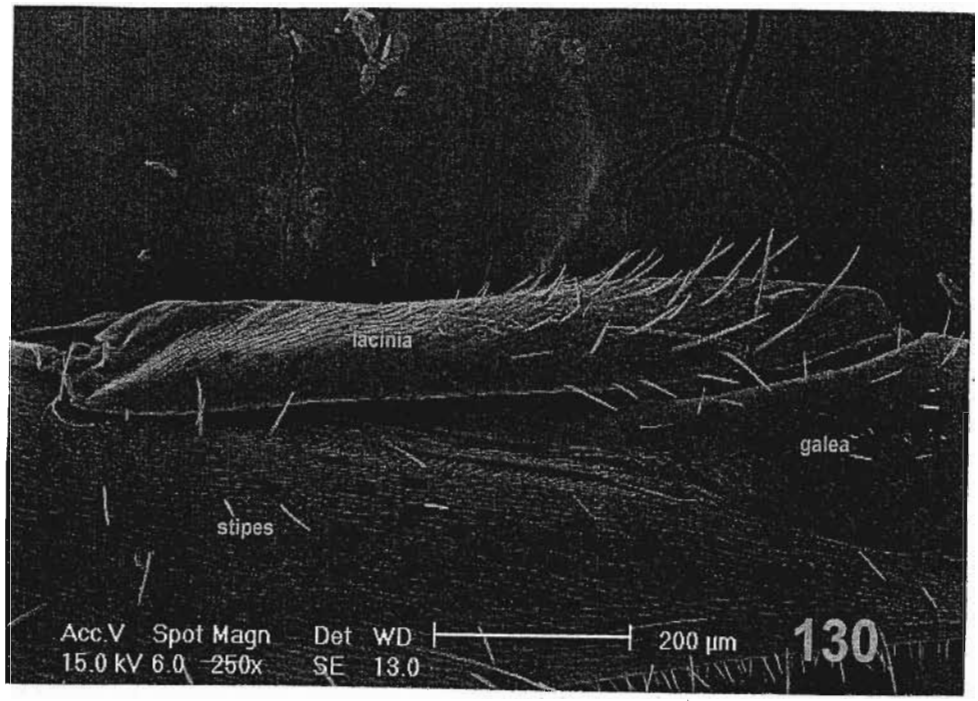


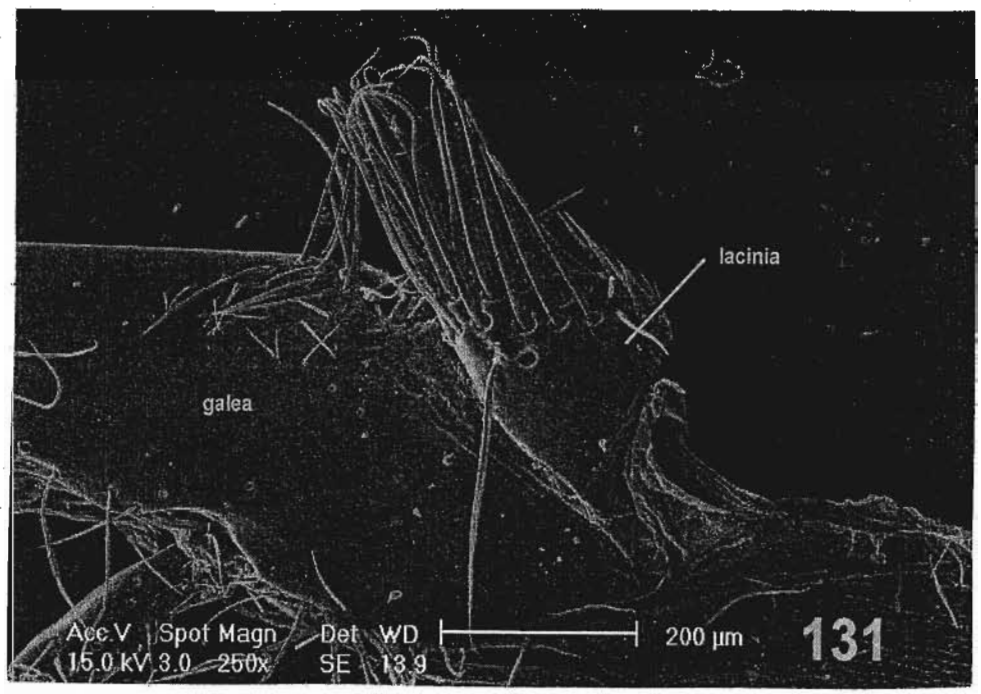


Figs 126-127. (126) Inner view of galea of *Colletes* species (note the primary and secondary ribs), (127) Inner view of galea of *Leioproctus* (*Nodocolletes*) species.

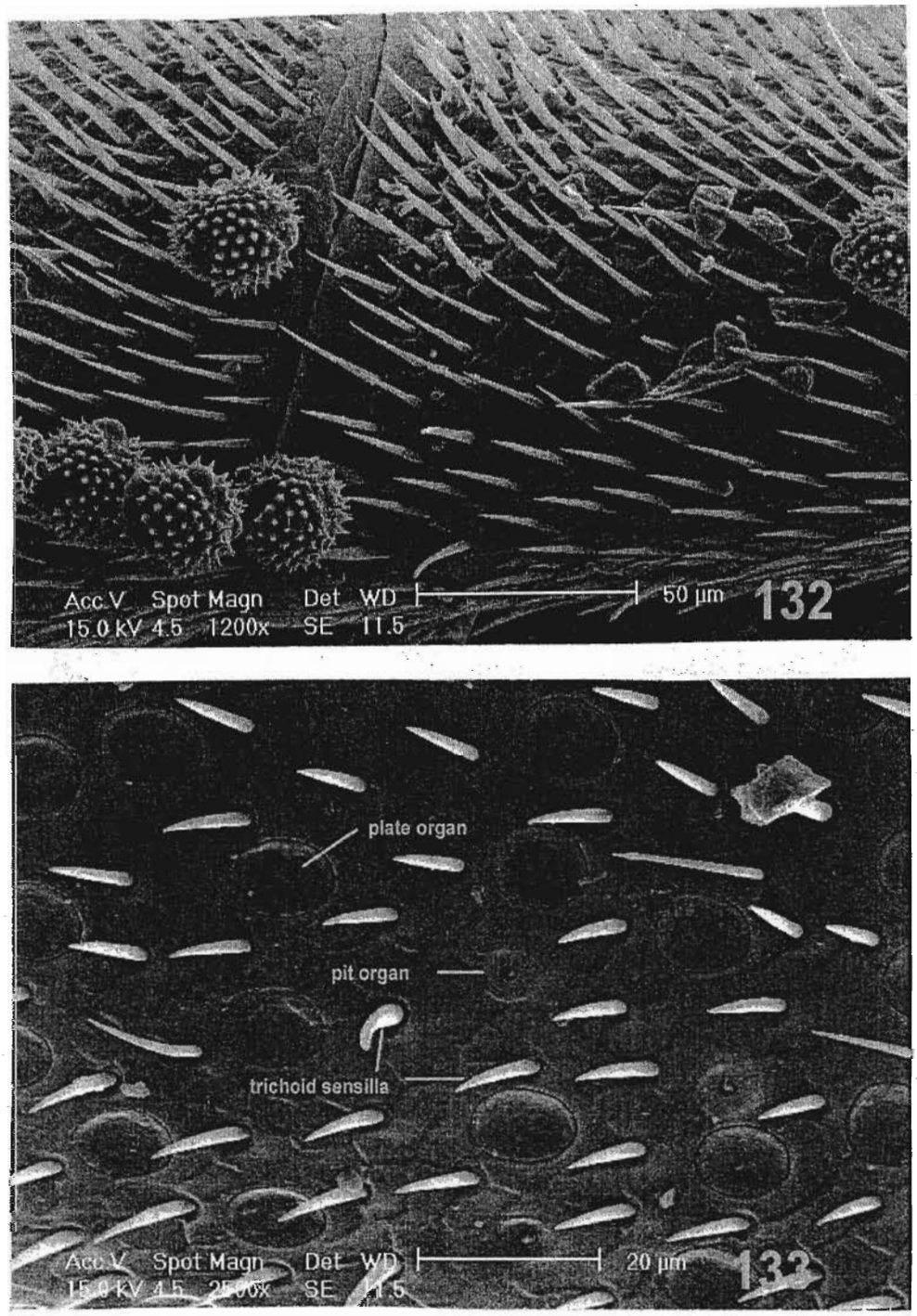


Figs 128-129. (128) Outer view of lacinia of female *Scrapter chloris* Eardley, (129) Outer view of lacinia of female *Scrapter nitidus* (Friese).

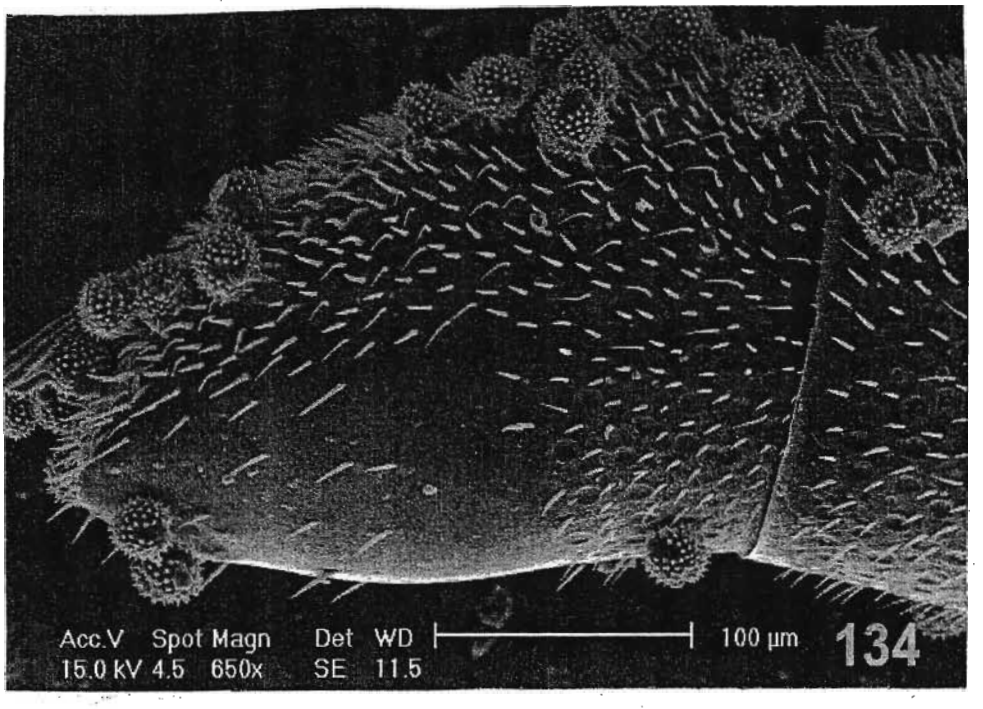


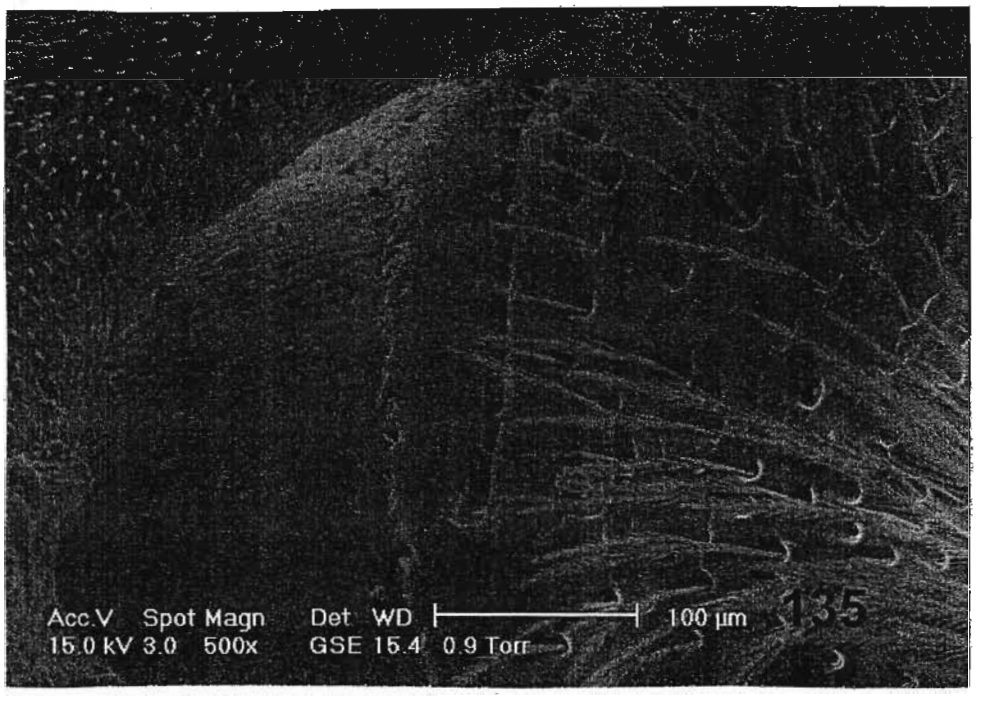


Figs 130-131. (130) Outer view of lacinia of female *Scrapter amplispinatus* Eardley, (131) Outer view of lacinia of *Leioproctus* (*Nodocolletes*) species.

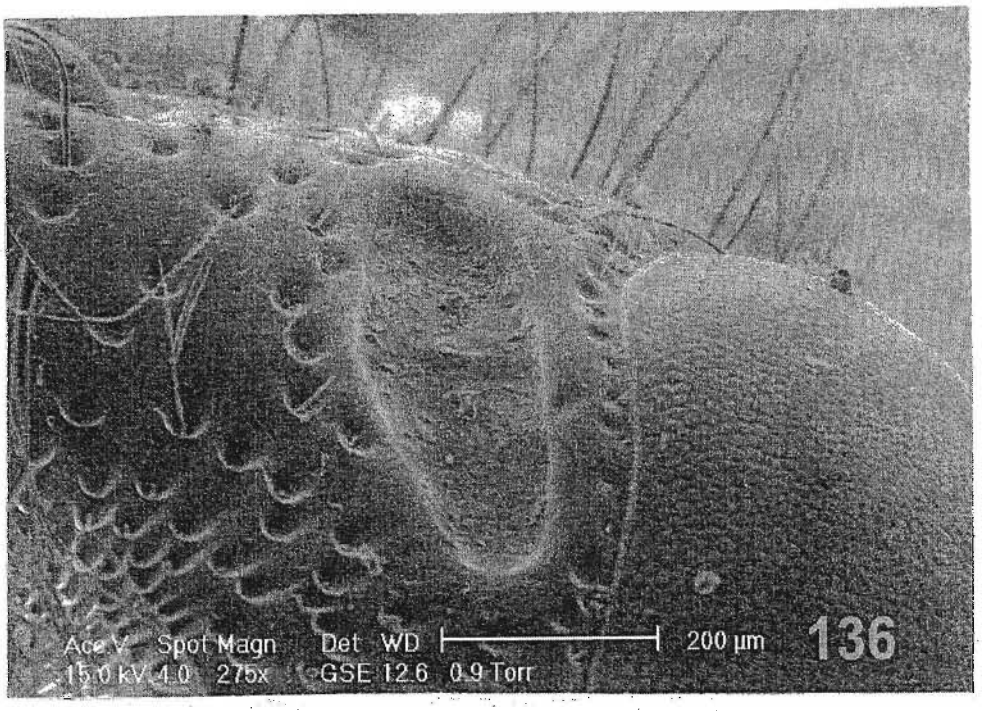


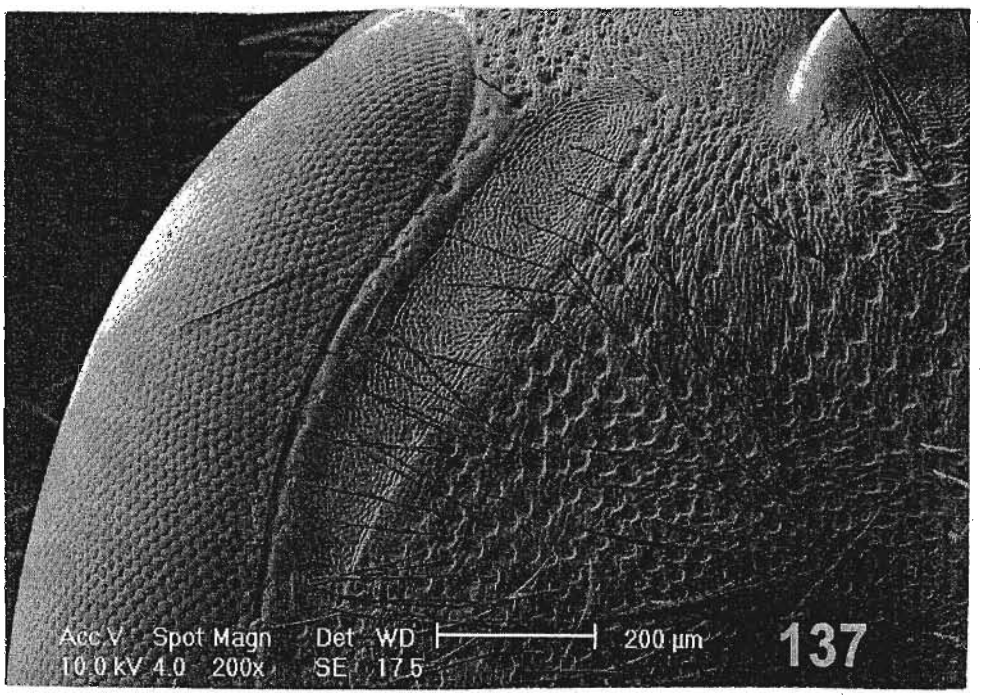
Figs 132-133. (132) Flagellomeres 1 and 2 of female *Scrapter nitidus* (Friese), (133) Flagellomere 9 of female *Scrapter nitidus* (Friese).



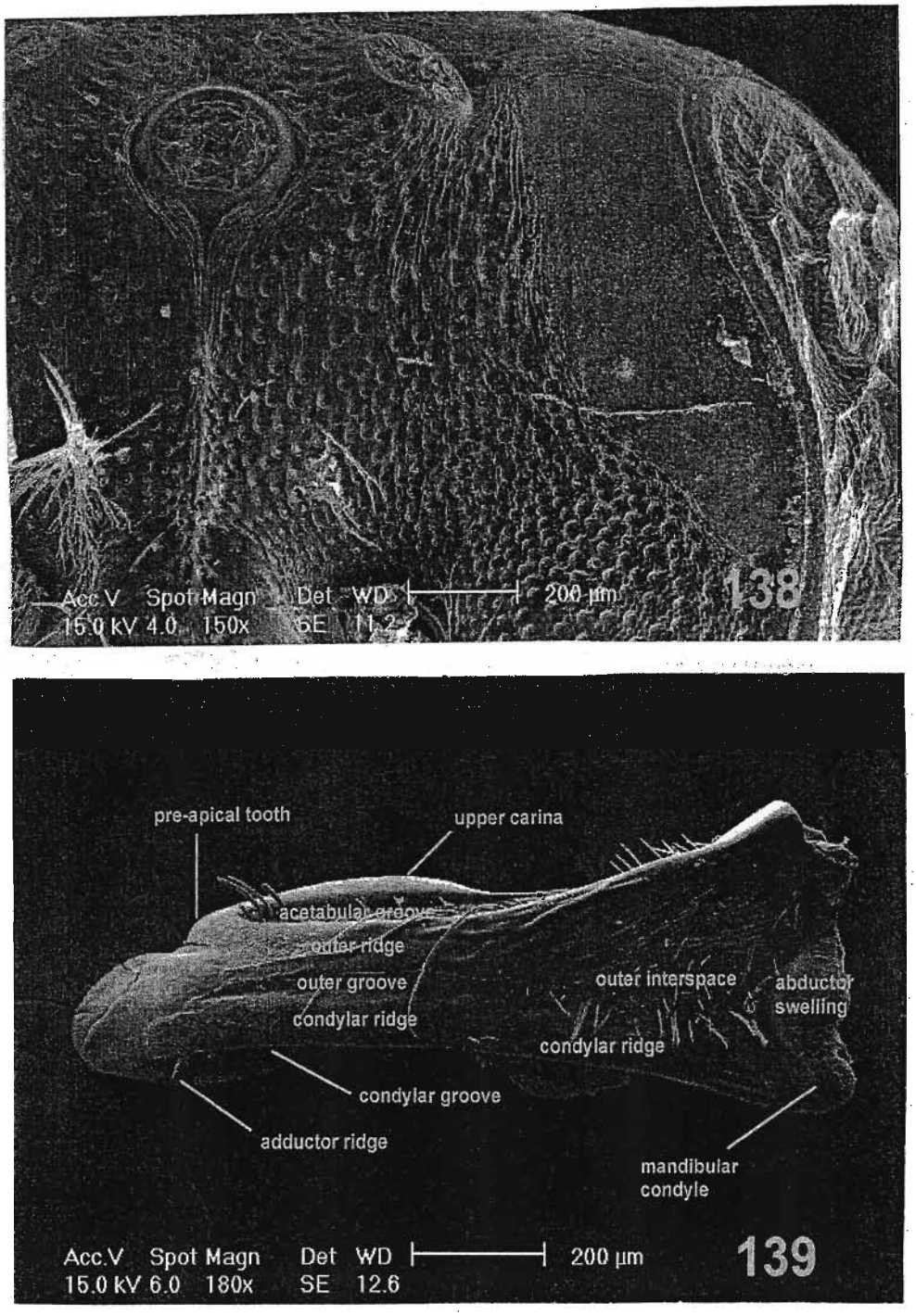


Figs 134-135. (134) Flagellomere 10 of female *Scrapter nitidus* (Friese), (135) Facial fovea of female *Scrapter nitidus* (Friese).

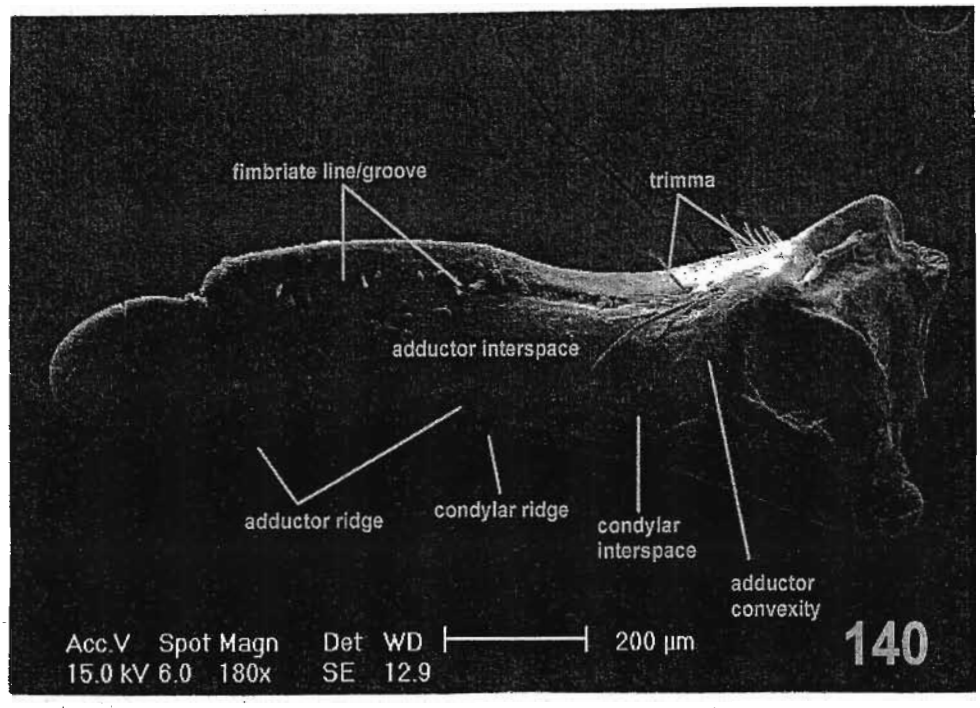


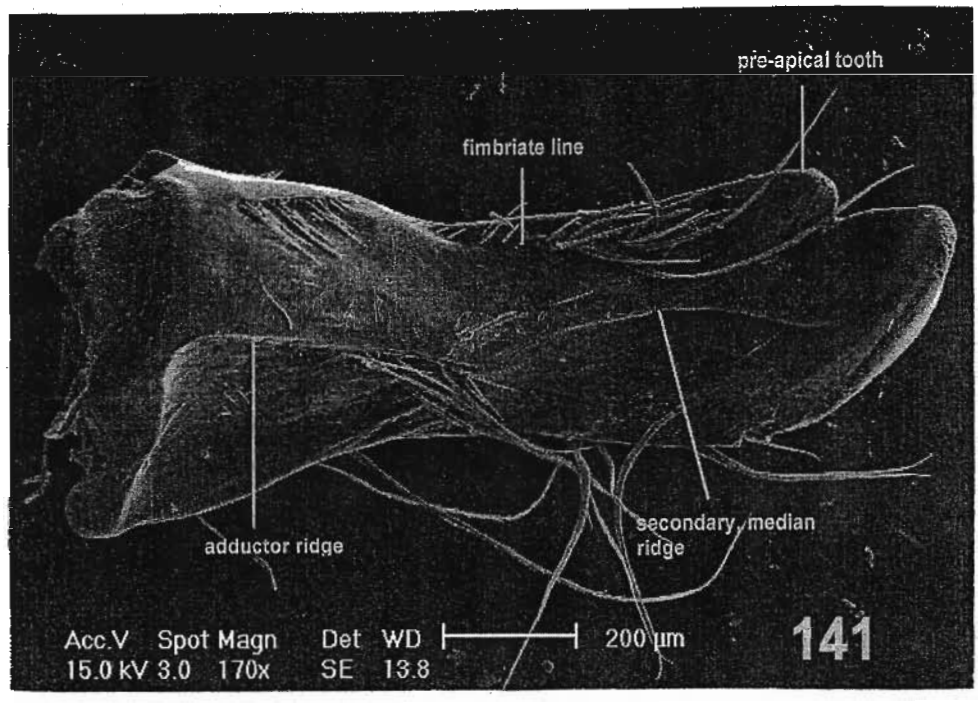


Figs 136-137. (136) Facial fovea of female *Scrapter basutorum* (Cockerell), (137) Facial fovea of female *Scrapter chloris* Eardley.

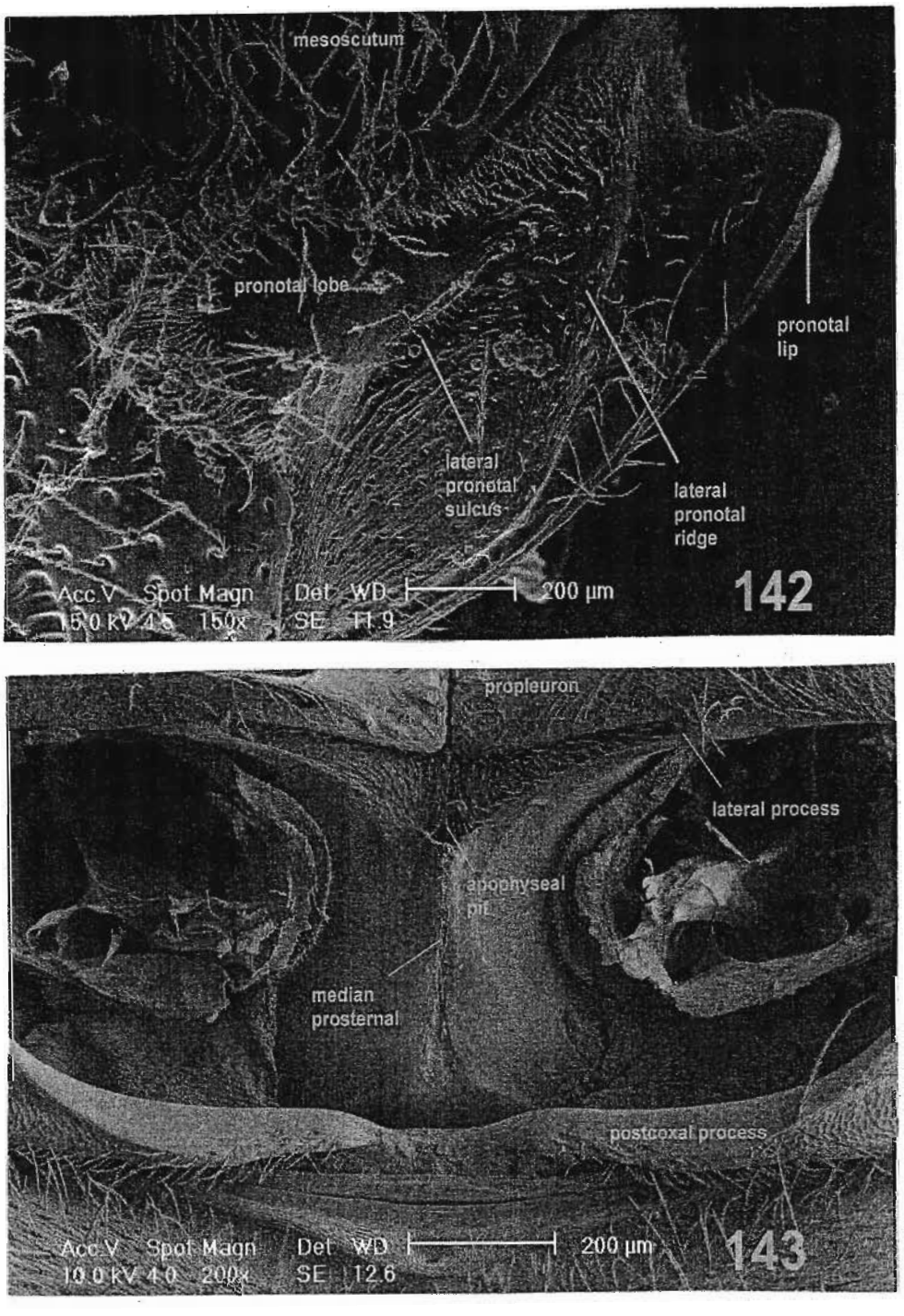


Figs 138-139. (138) Facial fovea of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (139) Outer view of left mandible of female *Scrapter algoensis* (Friese).

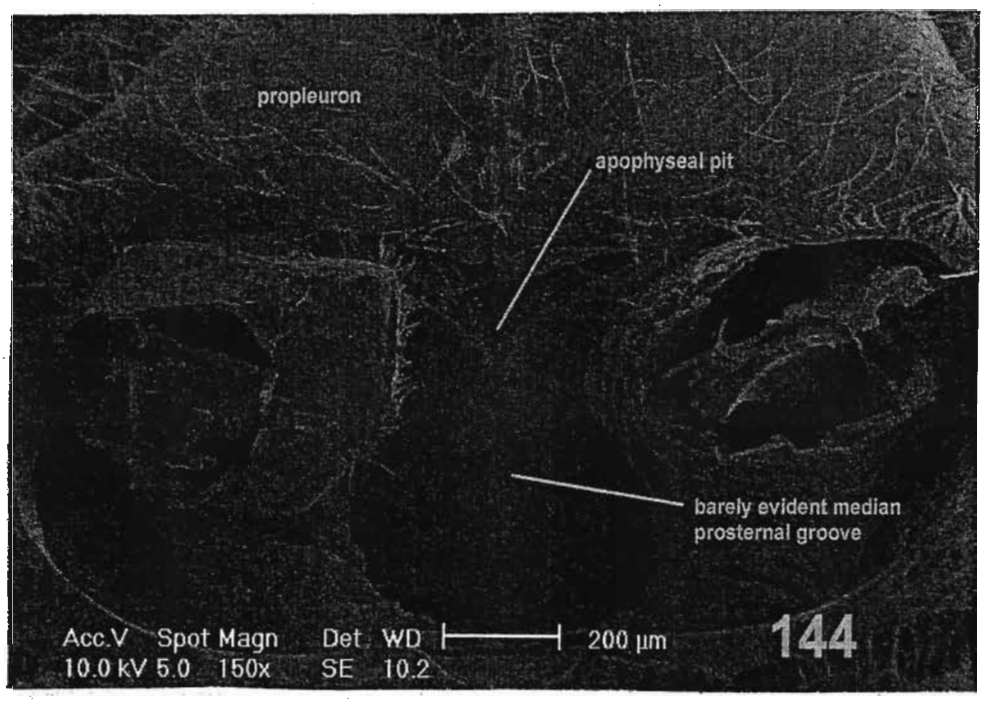


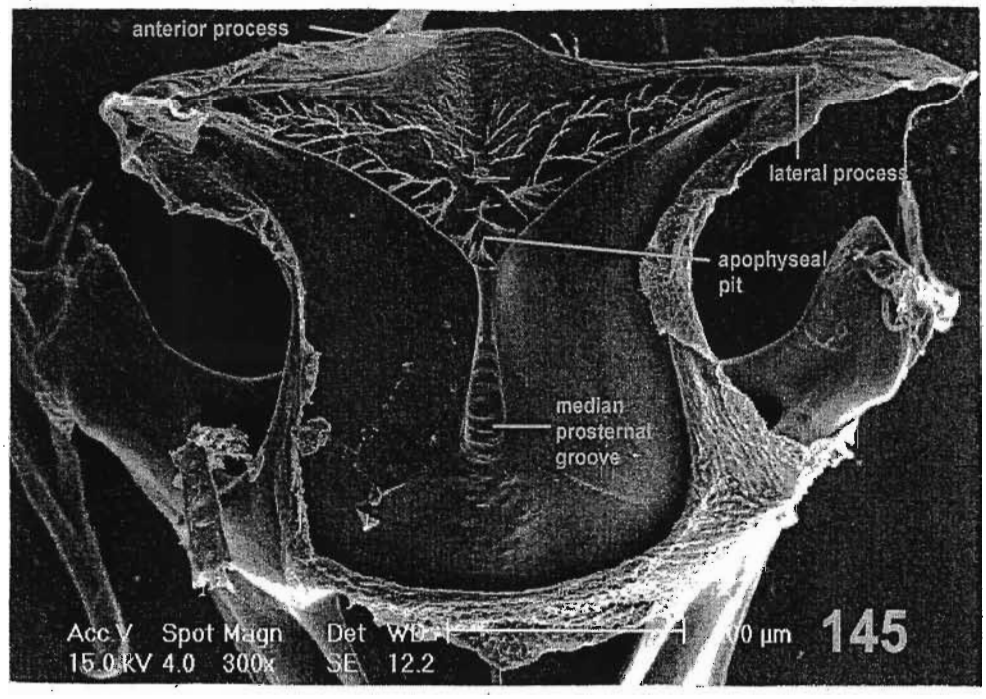


Figs 140-141. (140) Inner view of right mandible of female *Scrapter algoensis* (Friese), (141) Inner view of left mandible of *Colletes* species.

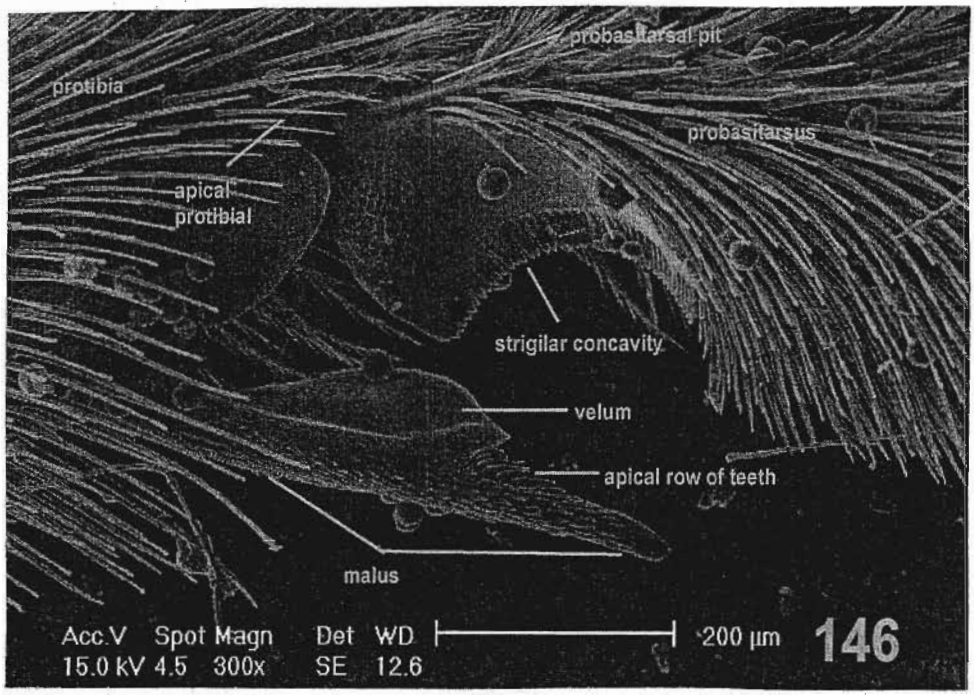


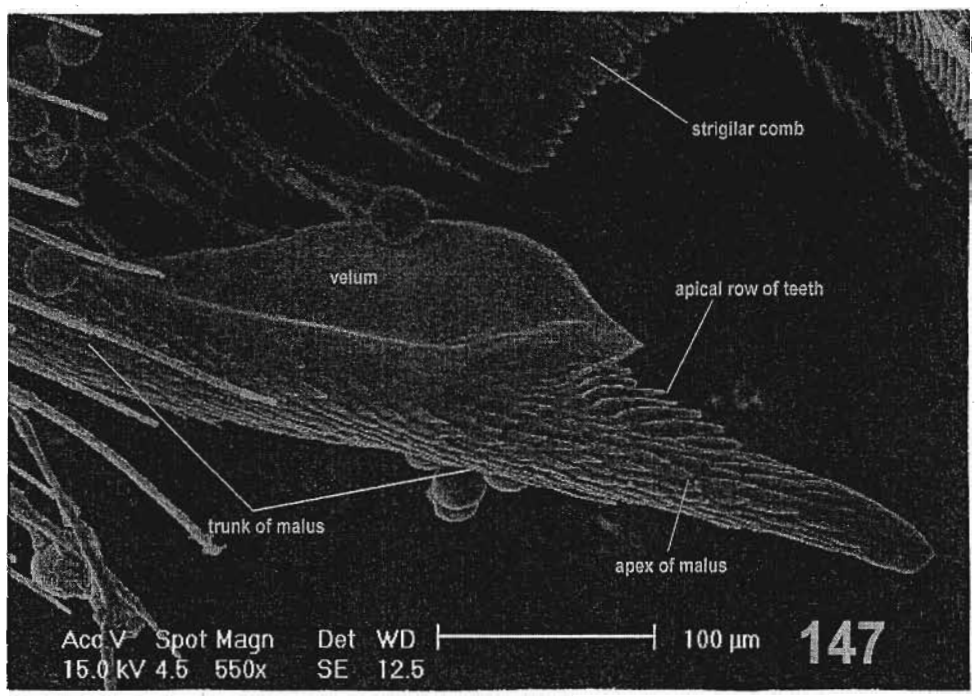
Figs 142-143. (142) Lateral view of pronotum of *Scrapter nitidus* (Friese) showing lateral pronotal ridge, (143) Prosternum of female *Scrapter chloris* Eardley.



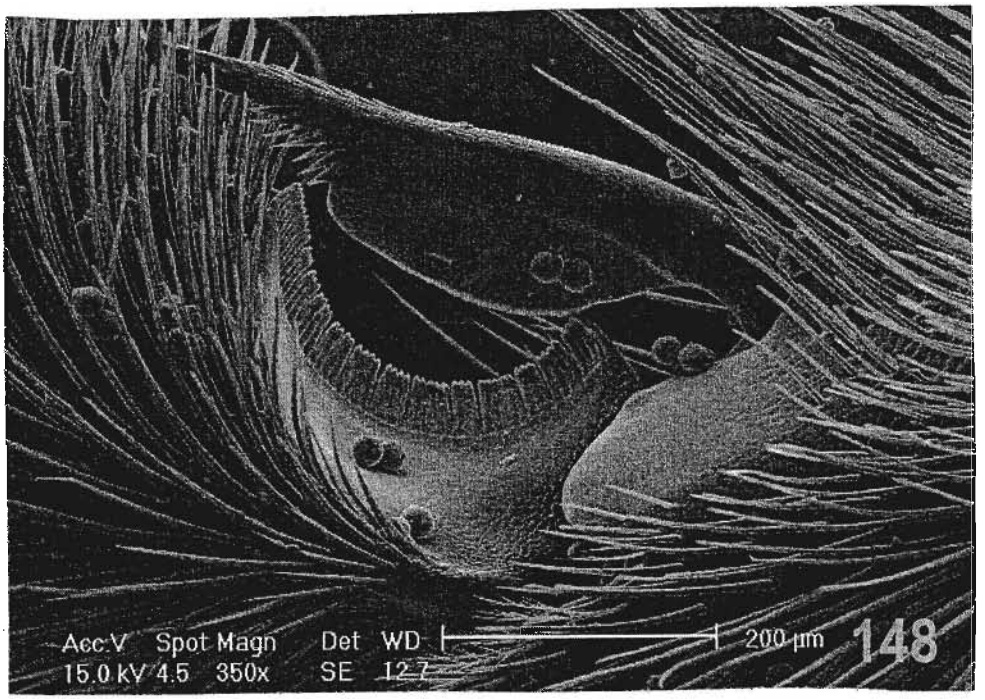


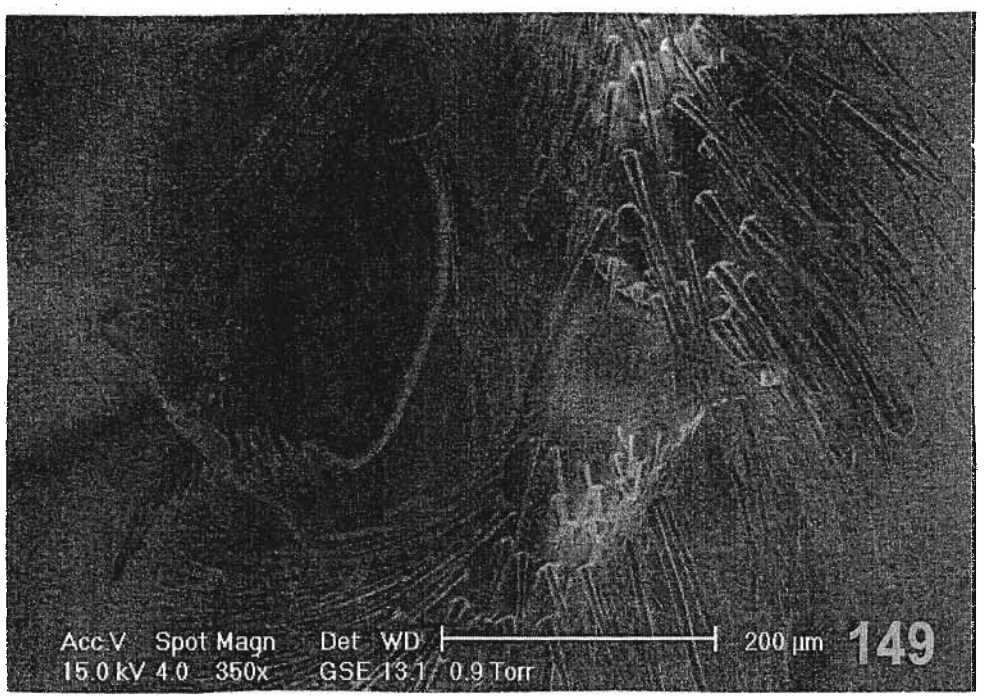
Figs 144-145. (144) Prosternum of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (145) Prosternum of female *Scrapter nitidus* (Friese).



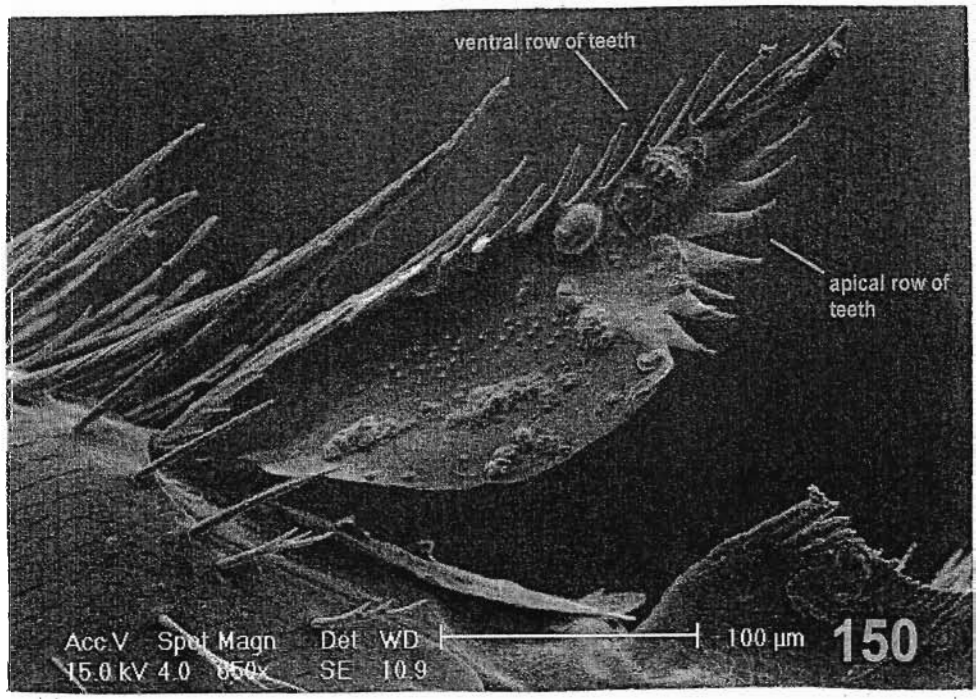


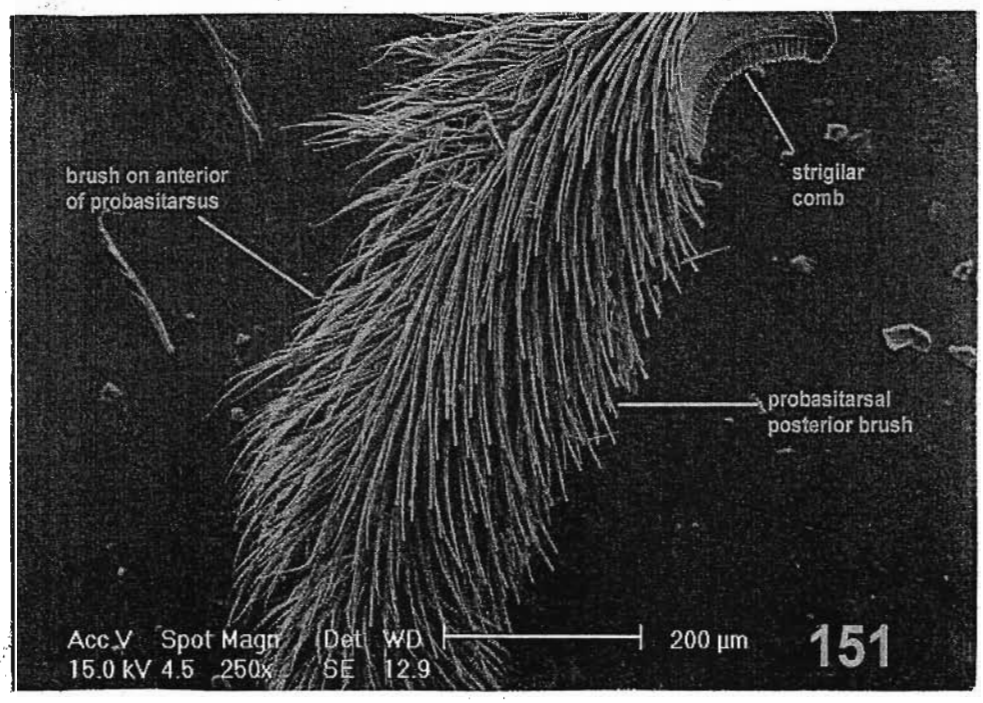
Figs 146-147. (146) Antenna cleaner of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (147) Another view of the antenna cleaner of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville.



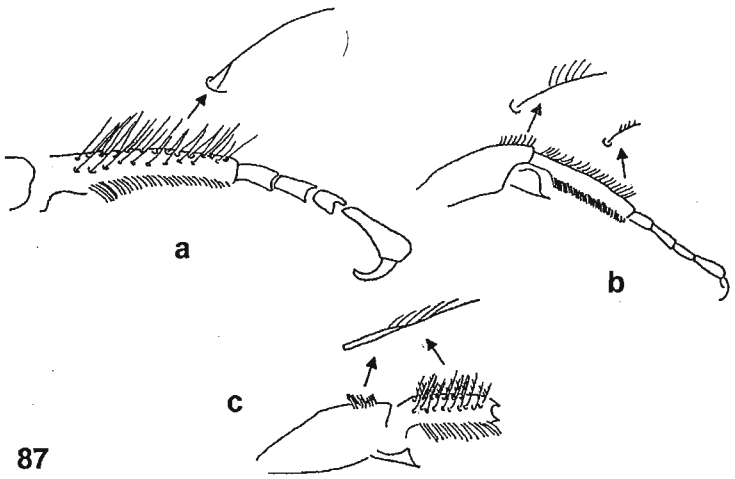


Figs 148-149. (148) Antenna cleaner of female *Scrapter amplispinatus* Eardley, (149) Antenna cleaner of female *Scrapter capensis* (Friese).

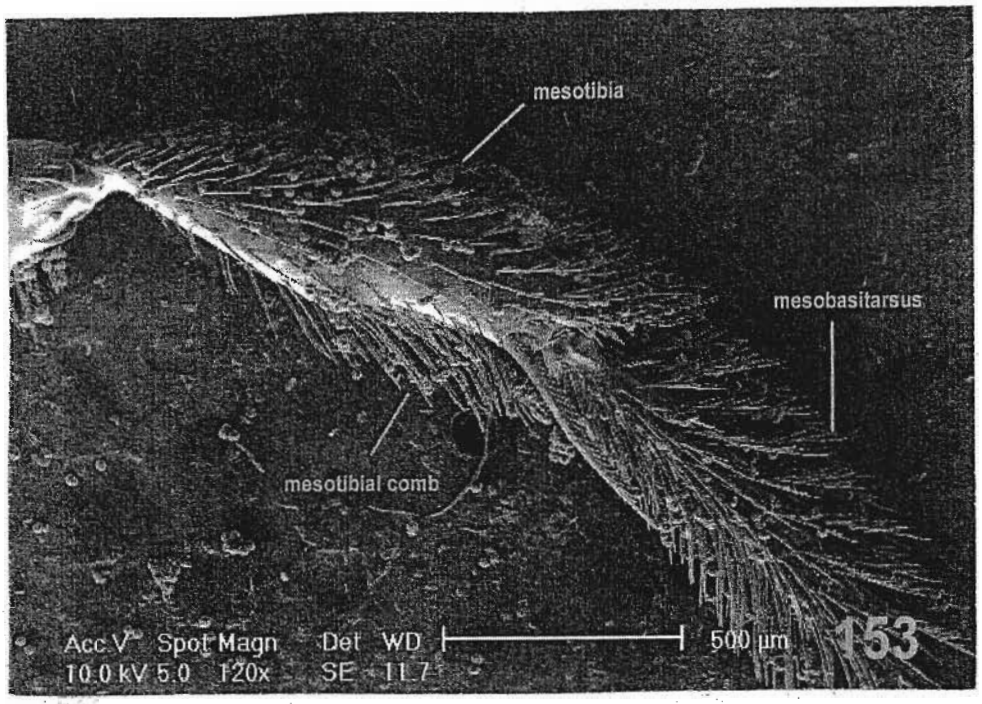


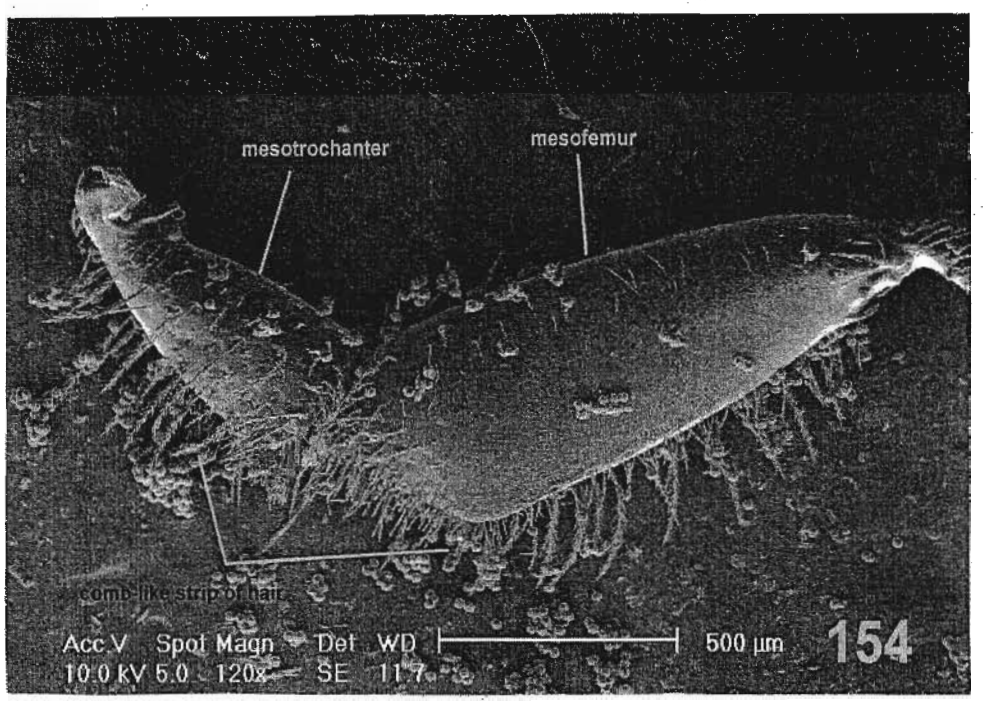


Figs 150-151. (150) Antenna cleaner of female *Scrapter flavostictus* Cockerell, (151) Probasitarsal brushes of female *Scrapter absonus* Eardley.

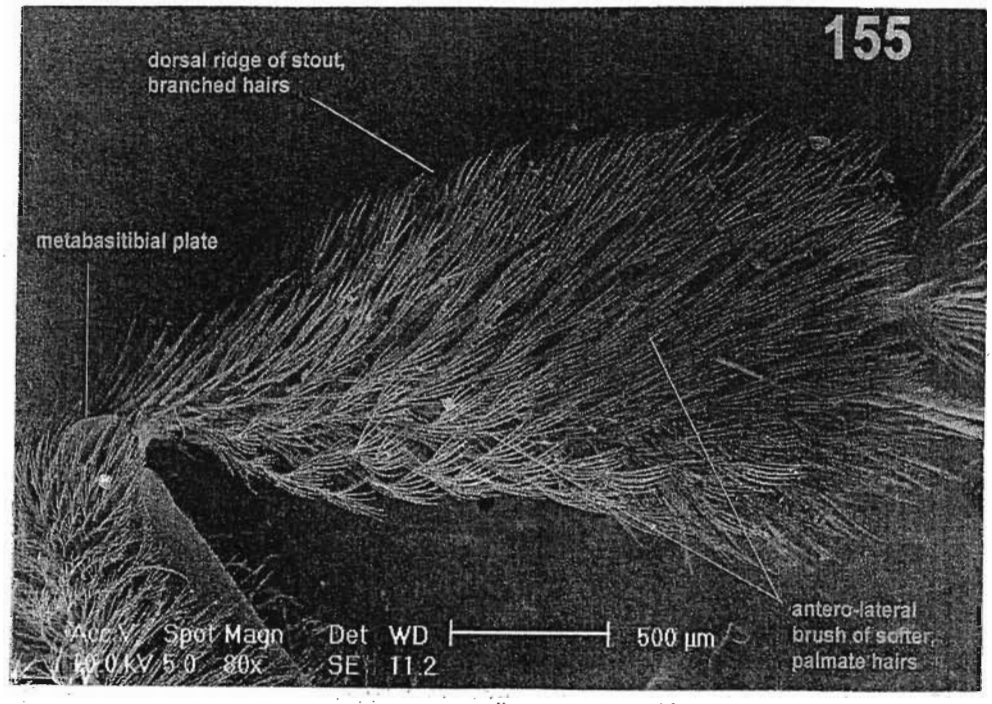


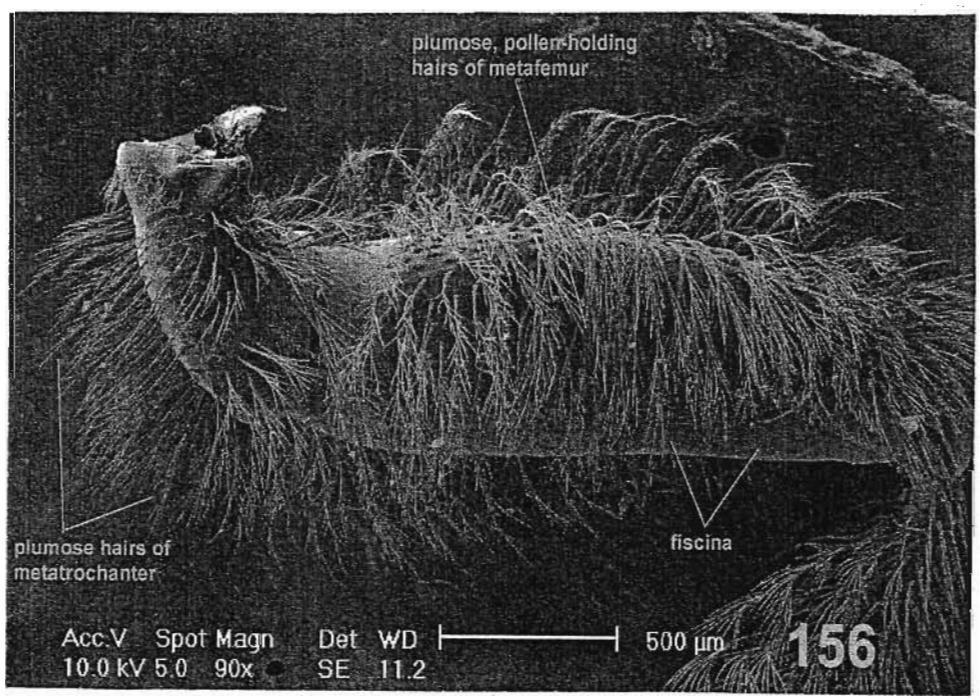
Figs 152 a-c. Lateral view of extended forelegs showing probasitarsal brushes, (a) *Scrapter basutorum* (Cockerell), (b) *S. bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (c) *S. heterodoxus* (Cockerell).



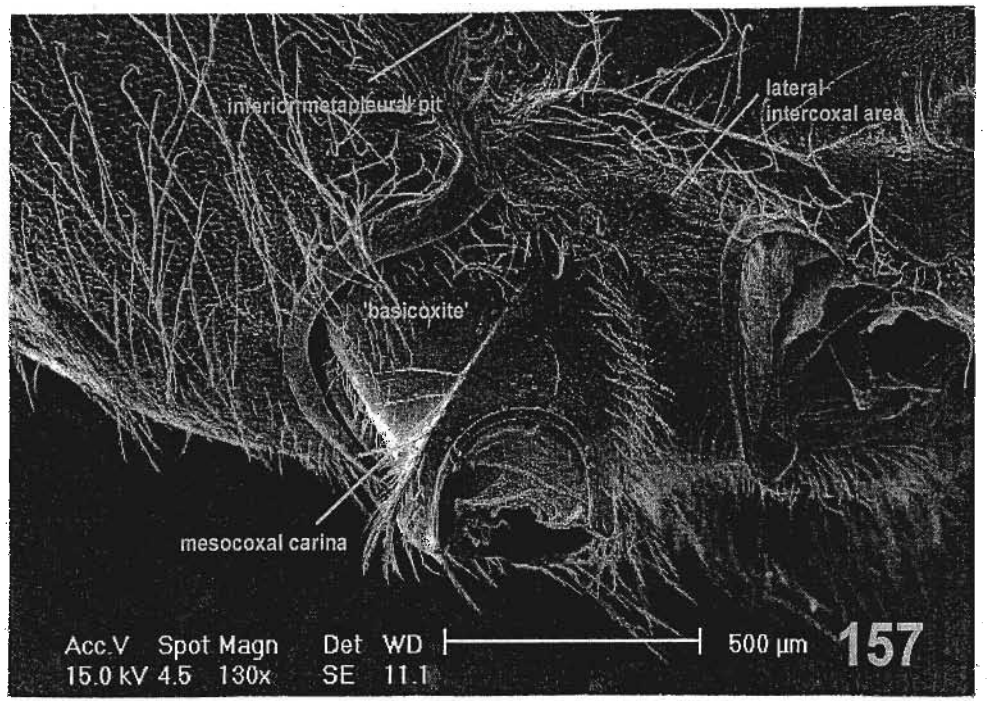


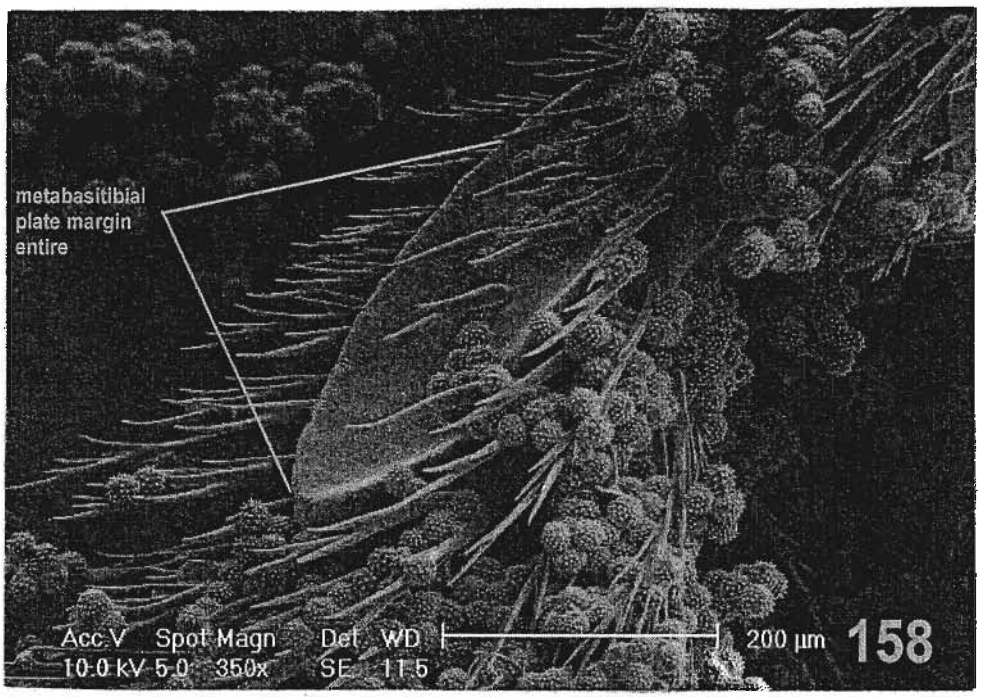
Figs 153-154. (153) Mesotibial comb of *Scrapter nitidus* (Friese), (154) Mesotrochanter and mesofemur of *Scrapter nitidus* (Friese).



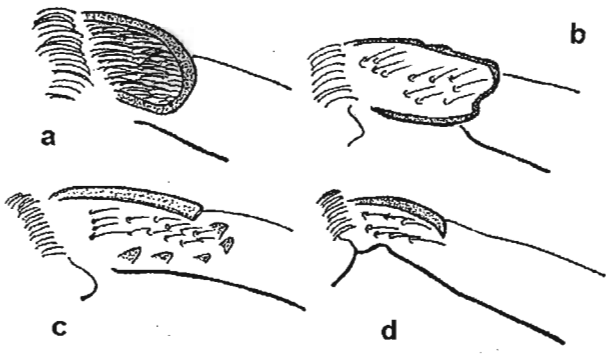


Figs 155-156. (155) Metatibial scopa of *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (156) Fiscina of *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville.

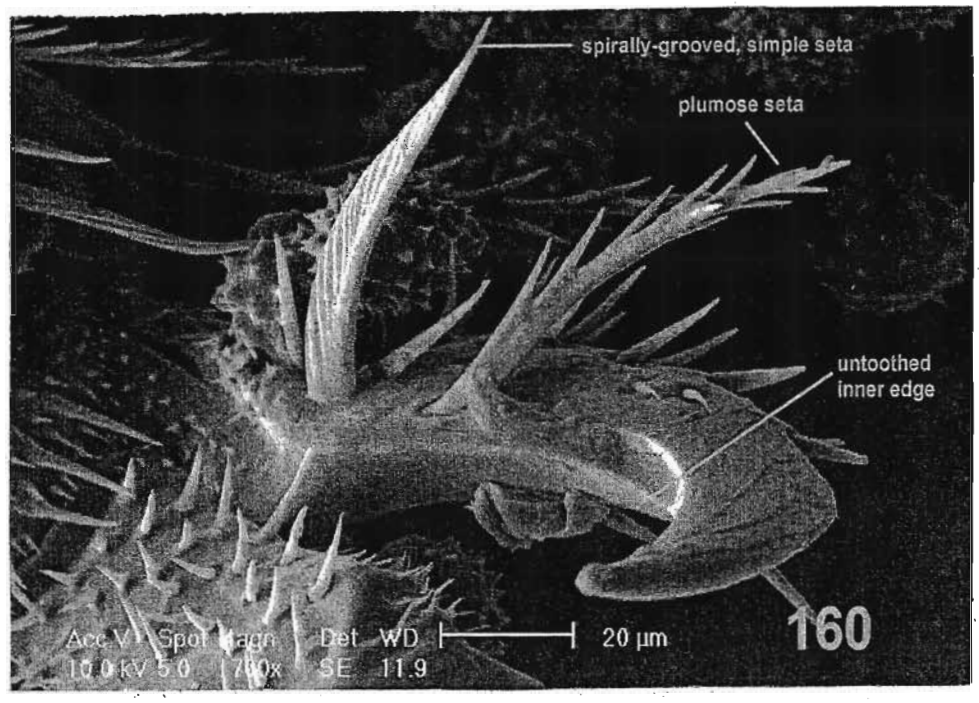


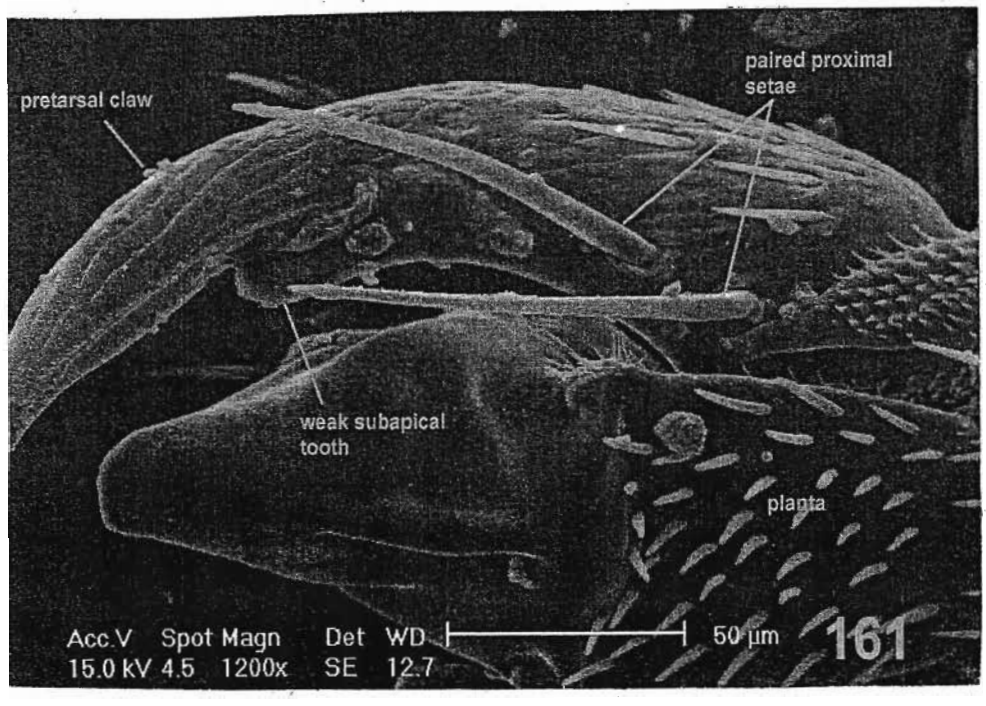


Figs 157-158. (157) Mesocoxa of *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (158) Metabasitibial plate of female *Scrapter nitidus* (Friese).

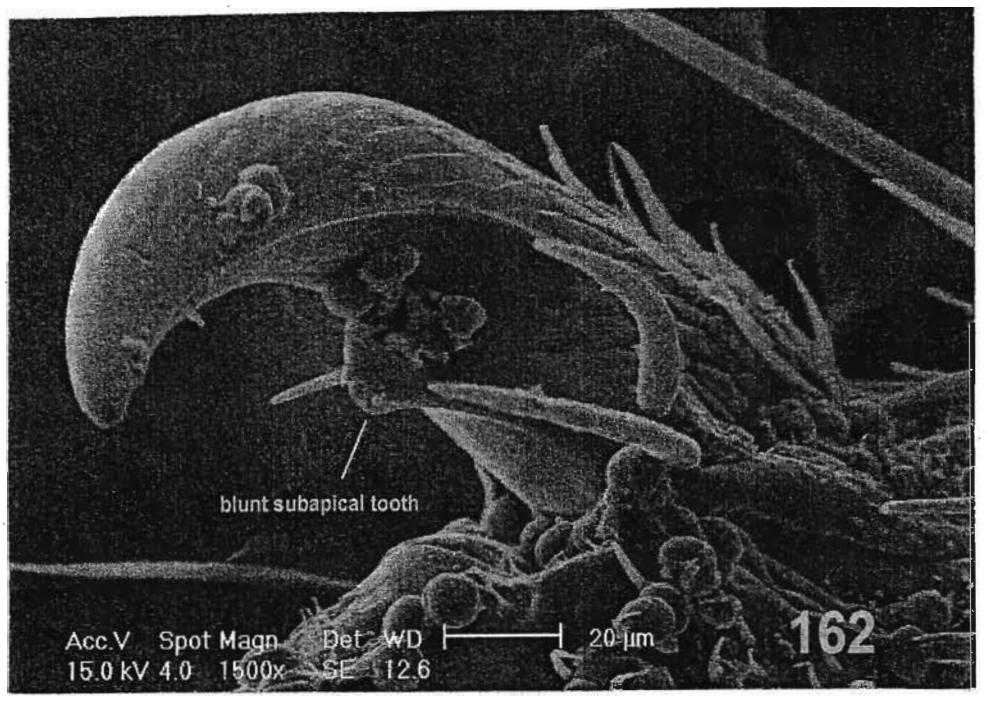


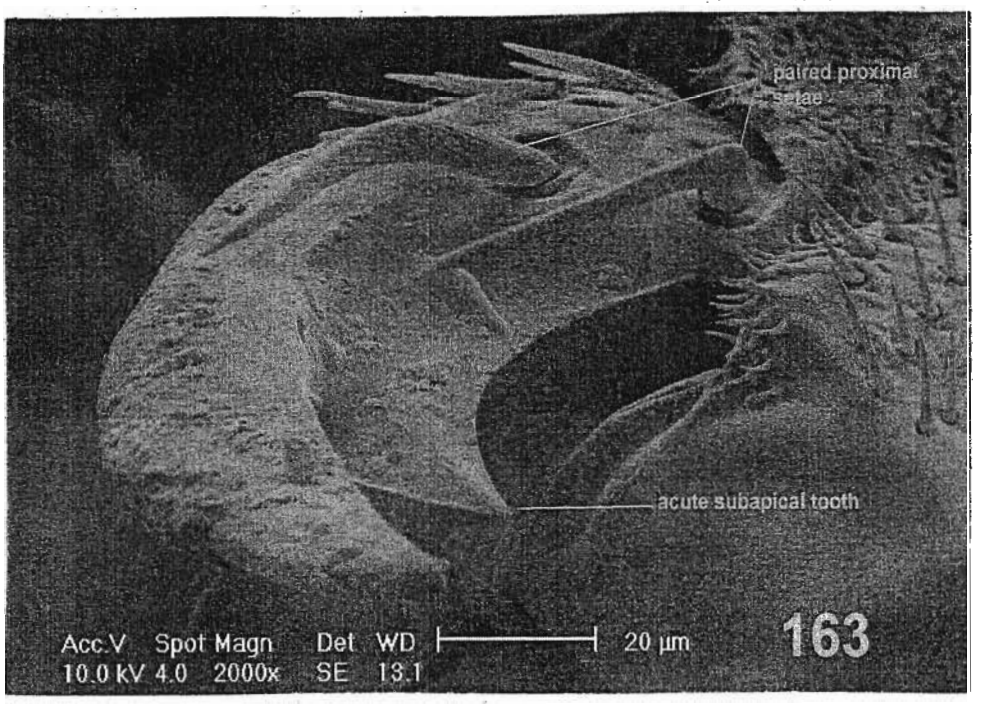
Figs 159 a-d. Anterior view of metabasitibial plates of *Scrapter* species: (a) female *S. armatipes* (Friese), (b) male *S. capensis* (Friese), (c) female *S. tomentum* Eardley, (d) male *S. algoensis* (Friese).



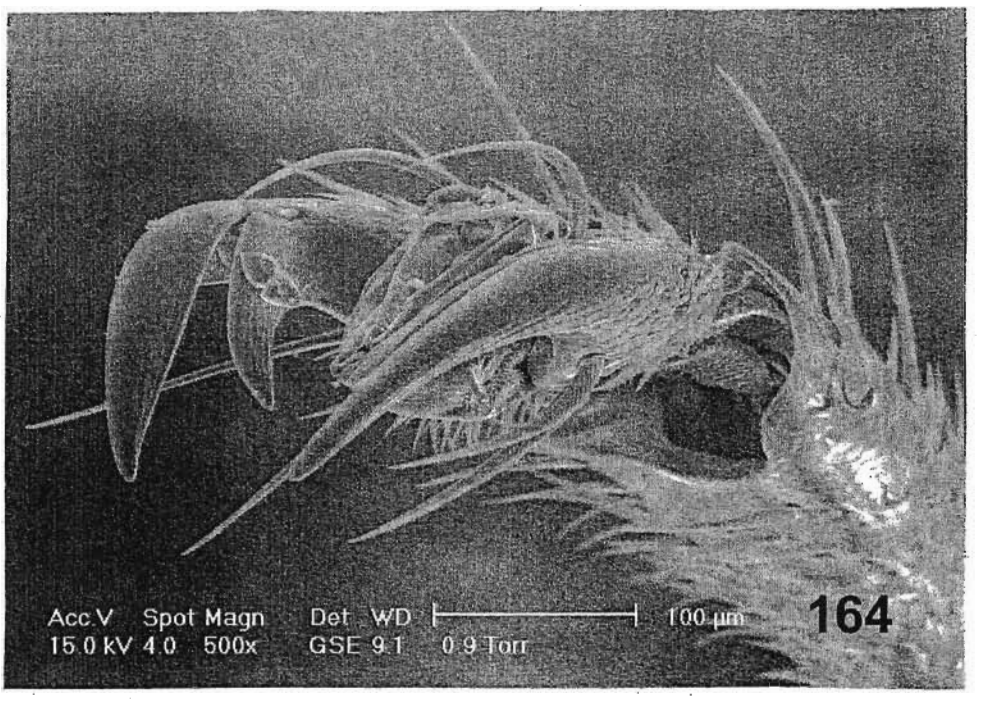


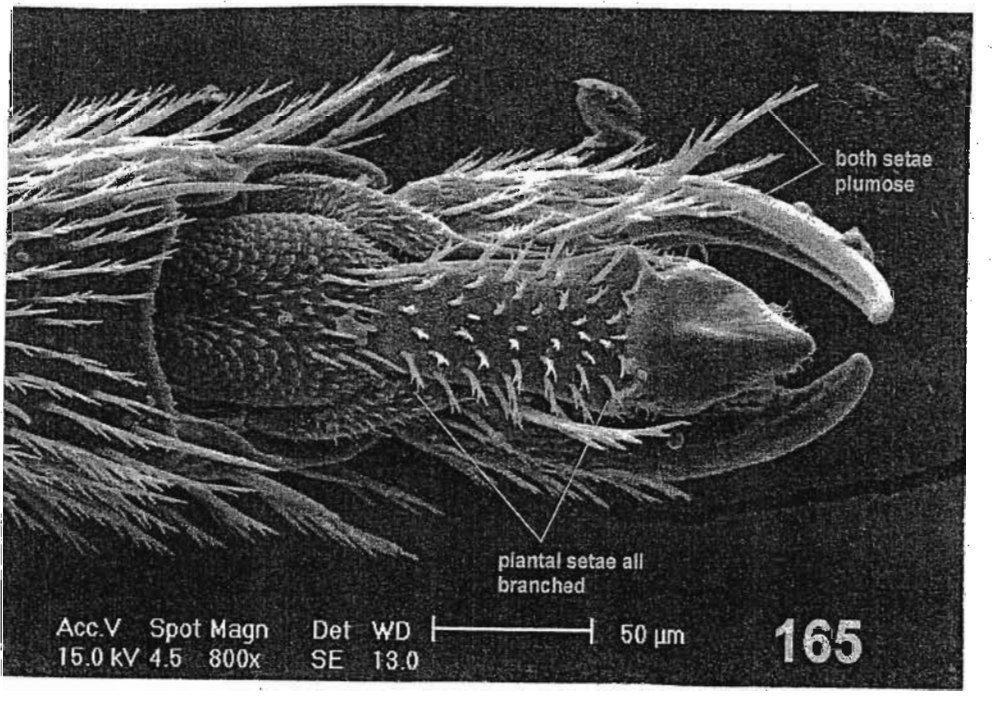
Figs 160-161. (160) Pretarsal claw and paired, proximal ungual setae of female *Scrapter nitidus* (Friese), (161) Pretarsal claw and paired, proximal ungual setae of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville.



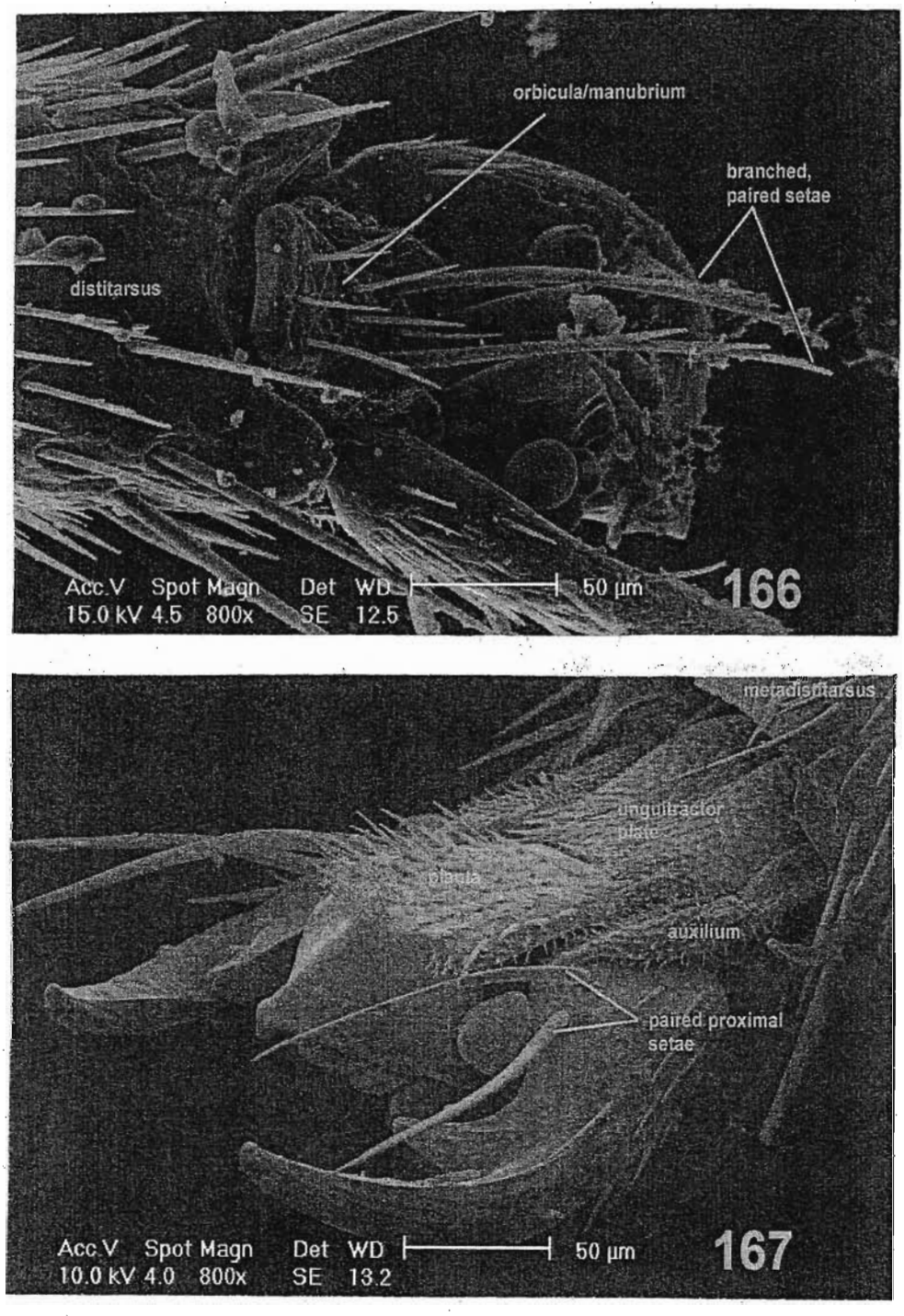


Figs 162-163. (162) Pretarsal claw and paired, proximal ungual setae of female *Scrapter tomentum* Eardley, (163) Pretarsal claw and paired, proximal ungual setae of female *Scrapter chloris* Eardley.

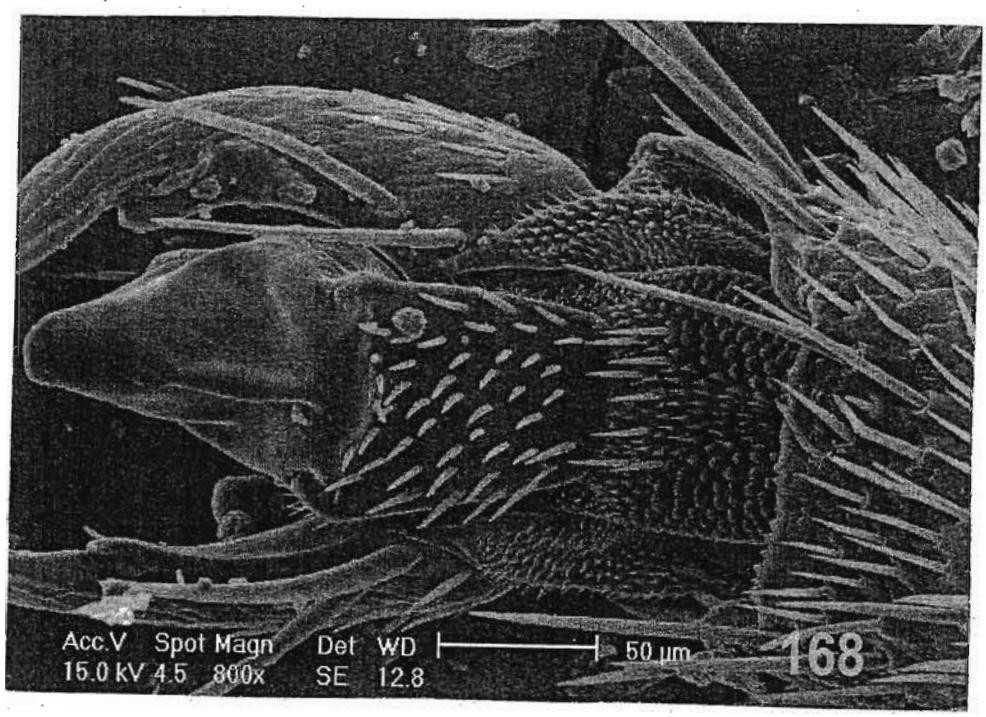


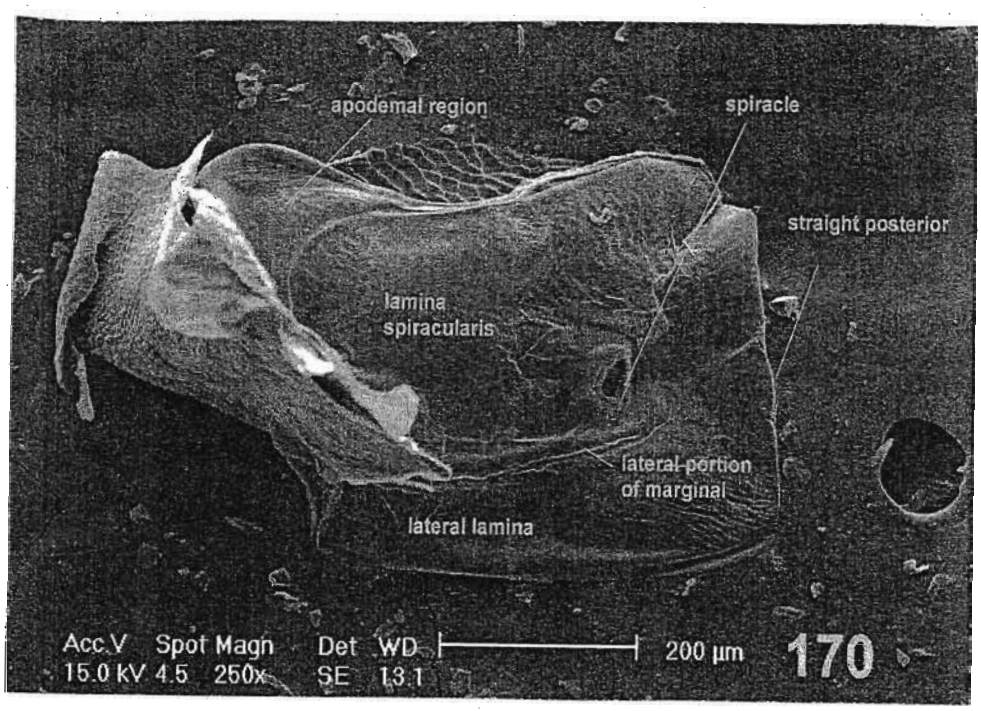


Figs 164-165. (164) Pretarsal claw and associated structures of female *Scrapter* cf. *erubescens* (Friese), (165) Ventral view of pretarsus of female *Scrapter armatipes* (Friese).



Figs 166-167. (166) Orbicula of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (167) Ventral view of pretarsus of female *Scrapter chloris* Eardley.





Figs 168, 170. (168) Ventral view of pretarsus of female *Scrapter bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, (170) Tergum 7 of female *Scrapter chloris* Eardley.

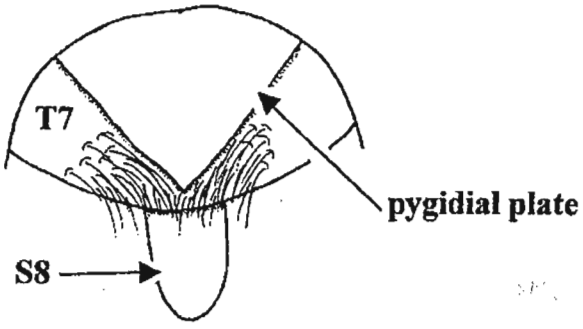
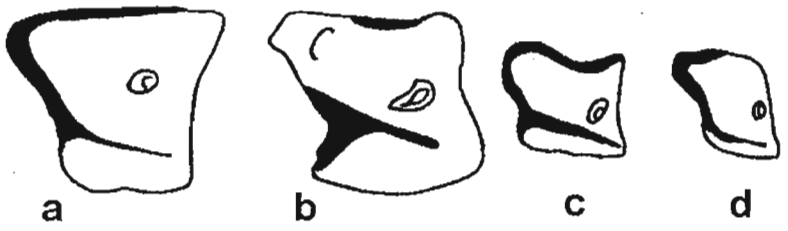


Fig. 169. Posterior view of tergum 7, pygidial plate and sternum 8 of male *Scrapter heterodoxus* (Cockerell).



Figs 171 a-d. Tergum 7 of female *Scrapter* species: (a) *S. heterodoxus* (Cockerell), (b) *S. niger* Lepeletier de Saint-Fargeau & Audinet-Serville, (c) *S. nitidus* (Friese), (d) *S. pruinosus*).

Figs 172-173. (172) Tergum 8 of female *Scrapter niger* Lepeletier de Saint-Fargeau & Audinet-Serville (left) and *S. heterodoxus* (Cockerell) (right), (173) Furcula of sting apparatus of *Scrapter chloris* Eardley.

Table 4. Adult morphological characters used in the cladistic analysis and their states.

Character number	Character description and states
1	Medio-longitudinal clypeal sulcus of M: (0) absent, (1) present
2	Labrum of F, distal area: (0) absent or greatly reduced, (1) apex constricted forming point ('snout-like'), (2) tapering gradually to a point or margin subtruncate
3	Labrum of F, basal area: (0) reduced, (1) smooth area with no medial depression, (2) smooth area with medial depression, (3) smooth and bituberculate, (4) narrow transverse ridge surmounted on smooth basal area
4	Postmentum of F: (0) flat plate and small sclerite, (1) moderately infolded plate and small sclerite, (2) folded sclerite composed of two 'panels' joined medially with a posterior process curling underneath
5	Inner eye orbits of M: (0) diverging dorsally, (1) parallel
6	Facial fovea of F: (0) broad and shallow, (1) narrow and shallow (bottom of fovea visible), (2) slit-like fovea (bottom of fovea not visible)
7	Pronotum of F: (0) no lateral ridge, (1) weak lateral ridge (not sharp-edged), (2) distinct lateral ridge (sharp-edged and prominent)
8	Mesoscutum sculpture of F: (0) smooth, (1) smooth with reticulation anteriorly, (2) finely roughened ('scaly'), (3) coarsely roughened ('leathery')
9	Propodeum of M: (0) declivitous, (1) angulate
10	Propodeum: (0) declivitous, (1) weakly to strongly angulate (basal area of propodeum discernable)
11	Propodeal triangle: (0) triangular, unmodified, (1) propodeal triangle lateral sides strongly incurved, corners forming three acute points
12	Anterior brush on probasitarsus of F: (0) all simple hairs, (1) mixture of branched and simple hairs, (2) all branched hairs
13	Antenna cleaner of F: (0) ventral row of teeth near-absent (barely evident at 50X magnification), (1) ventral row of teeth weak (discernable but not strong at 50X magnification) (2) ventral row of teeth strong (prominent at 50X magnification)
14	Pretarsal claws of F: (0) toothed, (1) simple
15	Paired, proximal ungual setae of pretarsus: (0) both setae simple, (1) one seta simple, the other branched, (2) both setae branched
16	Hairs on the ventral surface of the distitarsus and planta: (0) hairs simple on both, (1) branched hairs present on distitarsus and simple hairs on planta, (2) simple hairs on distitarsus, branched hairs on planta, (3) branched hairs on both distitarsus and planta
17	Shape of M metabasitibial plate: (0) entire, (1) near-entire (slight notch or gap distally), (2) posterior carina and anterior tubercles, (3) posterior carina only, (4) ring of tubercles only, (5) absent
18	Shape of F metabasitibial plate: (0) entire, (1) near-entire but notched apically, (2) approximately three lanceolate blades, (3) posterior carina only, (4) ring of tubercles only, (5) absent
19	Metafemur of M: (0) unmodified, sides approximately parallel, (1) grossly swollen
20	Metatibia of M: (0) unmodified, sides approximately parallel, (1) tuberculate, (2) spurred distally
21	Hair bands along graduli of terga in F: (0) absent, (1) bands present along graduli on T2-T3, (2) bands present along graduli on T2-T4, (3) bands present along graduli on T3-T4, (4) bands present along graduli on T2-T5

Table 5. Data matrix for *Scrapter* species based on 25 characters as in Table 4.

	1	2	3	4	5	6	7	8	9
S. nitidus	1	1	2	2	0	2	1	0	1
S. ruficornis	1	1	2	2	0	2	0	0	1
S. opacus	1	1	2	2	0	2	0	0	1
S. basutorum	1	1	2	2	0	0	0	0	1
S. flavipes	0	1	0	2	0	1	1	0	1
S. pallidipennis	1	1	2	2	0	0	0	0	1
S. flavostictus	1	1	2	2	0	0	0	0	1
S. albitarsis	0	?	?	0	0	1	0	2	1
S. absonus	0	2	2	0	0	0	0	2	1
S. avius	0	0	1	0	1	1	2	0	1
S. calx	0	2	1	0	0	1	2	2	1
S. caesariatus	0	0	1	2	0	0	0	0	1
S. aureiferus	0	2	1	0	0	1	1	0	1
S. heterodoxus	1	1	1	2	0	0	0	0	0
S. bicolor	0	0	2	1	1	0	0	2	0
S. whiteheadi	0	2	1	0	-	0	1	1	-
S. niger	0	2	1	0	0	0	0	1	1
S. leonis	0	2	1	0	-	0	0	0	-
S. thoracicus	0	?	?	?	1	0	?	?	0
S. tomentum	0	2	1	0	1	0	0	0	1
S. algoensis	0	2	2	0	1	0	2	2	1
S. albifumus	0	2	3	0	1	1	2	2	1
S. chloris	0	2	2	0	1	0	1	3	0
S. luridus	0	2	2	0	1	0	1	3	1
S. erubescens	0	2	2	2	0	0	0	0	0
S. fuliginatus	0	?	?	?	0	0	?	?	0
S. amplispinatus	0	2	2	2	0	0	0	2	0
S. striatus	0	?	?	0	0	0	0	0	1
S. capensis	0	2	2	0	0	0	0	2	0
S. acanthophorus	0	-	-	-	1	-	-	-	1
S. carysomus	0	-	-	-	0	-	-	-	1
S. catoxys	0	2	1	0	0	1	?	0	1
S. chrysomastes	0	-	-	-	1	-	-	-	1
S. eremanthedon	0	?	?	?	1	1	0	2	1
S. glarea	0	-	-	-	0	-	-	-	1
S. oxyaspis	0	-	-	-	0	-	-	-	0
S. sittybon	0	-	-	-	0	-	-	-	1
S. pruinosus	0	2	3	0	0	1	1	0	1
S. pyretus	0	2	2	?	0	1	1	2	1
S. armatipes	0	2	?	0	0	0	0	0	0
S. amplitarsus	0	2	1	0	0	0	0	2	1
S. viciniger	0	-	-	-	0	0	-	-	0
Colletes sp.	0	2	1	2	0	0	2	3	0
Euryglossa sp.	0	2	4	0	1	2	0	0	0
Hylaeus sp.	0	0	1	0	1	2	0	2	0

- = not applicable i.e. respective sex of the species is unknown

Table 5 continued.

	10	11	12	13	14	15	16	17
S. nitidus	1	0	1	2	1	1	1	0
S. ruficornis	1	0	2	2	1	1	1	3
S. opacus	1	0	2	1	1	0	?	3
S. basutorum	1	0	0	2	1	0	3	0
S. flavipes	1	0	0	2	1	1	3	3
S. pallidipennis	1	0	1	1	1	1	?	3
S. flavostictus	1	0	0	2	1	0	0	3
S. albitarsis	1	0	?	?	1	0	?	0
S. absonus	1	0	2	1	0	0	0	0
S. avius	1	0	2	1	1	0	0	3
S. calx	1	0	2	2	1	1	?	3
S. caesariatus	1	0	0	1	0	0	0	0
S. aureiferus	1	0	2	2	1	1	0	3
S. heterodoxus	0	0	2	2	1	1	0	4
S. bicolor	0	0	2	1	0	0	0	3
S. whiteheadi	1	0	1	0	0	0	0	-
S. niger	1	0	0	1	1	0	0	2
S. leonis	1	0	1	1	0	0	?	-
S. thoracicus	0	0	?	?	1	?	?	1
S. tomentum	1	0	0	1	0	0	0	2
S. algoensis	1	0	1	1	0	0	0	3
S. albifumus	1	0	0	?	0	0	?	0
S. chloris	0	0	1	0	0	0	0	2
S. luridus	0	0	1	0	0	0	0	0
S. erubescens	0	1	1	1	1	0	0	3
S. fuliginatus	0	1	?	?	1	?	?	?
S. amplispinatus	0	1	0	1	1	0	0	0
S. striatus	1	0	0	1	1	1	0	2
S. capensis	0	0	1	1	0	0	0	1
S. acanthophorus	1	0	-	-	-	-	-	0
S. carysomus	1	0	-	-	-	-	-	0
S. catoxys	1	0	2	1	?	1	?	0
S. chrysomastes	1	0	-	-	-	-	-	3
S. eremanthedon	1	0	0	?	0	-	-	0
S. glarea	1	0	-	-	-	-	-	0
S. oxyaspis	0	0	-	-	-	-	-	0
S. sittybon	1	0	-	-	-	-	-	0
S. pruinosus	1	0	1	2	0	0	?	3
S. pyretus	1	0	0	2	1	0	?	3
S. armatipes	1	0	1	2	1	2	3	0
S. amplitarsus	1	0	1	2	1	0	2	0
S. viciniger	0	0	-	-	-	-	-	0
Colletes sp.	0	0	0	2	0	0	0	5
Euryglossa sp.	0	0	0	2	0	0	0	4
Hylaeus sp.	0	0	0	2	0	0	0	5

Table 5 continued

	18	19	20	21	22	23	24	25
S. nitidus	0	0	0	0	0	1	1	1
S. ruficornis	0	0	0	0	0	0	1	0
S. opacus	0	0	0	0	0	0	1	1
S. basutorum	0	0	0	0	0	0	1	0
S. flavipes	0	0	0	0	0	1	1	1
S. pallidipennis	0	0	0	0	0	0	1	0
S. flavostictus	0	0	0	0	0	0	1	?
S. albitarsis	0	0	0	0	0	0	1	0
S. absonus	4	0	0	0	0	0	2	0
S. avius	4	0	0	0	0	4	1	0
S. calx	0	0	0	1	4	0	1	0
S. caesariatus	1	0	0	0	0	0	1	0
S. aureiferus	3	1	1	0	3	0	1	0
S. heterodoxus	1	1	1	0	2	0	3	1
S. bicolor	4	0	0	0	0	5	2	0
S. whiteheadi	4	0	0	0	0	7	3	-
S. niger	4	0	0	0	0	0	2	0
S. leonis	4	0	0	0	0	0	2	-
S. thoracicus	?	0	0	?	?	0	2	1
S. tomentum	4	0	0	4	1	0	0	0
S. algoensis	4	0	0	3	3	0	2	1
S. albifumus	0	0	0	2	0	0	0	?
S. chloris	4	0	0	0	0	6	3	0
S. luridus	4	0	0	0	0	6	3	0
S. erubescens	0	0	0	0	0	4	3	1
S. fuliginatus	?	0	0	?	?	0	3	1
S. amplispinatus	4	0	0	0	1	0	3	1
S. striatus	2	0	0	?	0	0	?	1
S. capensis	0	0	0	0	0	0	?	0
S. acanthophorus	-	0	1	-	-	-	-	1
S. carysomus	-	0	0	-	-	-	-	1
S. catoxys	0	0	0	0	0	0	1	0
S. chrysomastes	-	0	0	-	-	-	-	0
S. eremanthedon	?	0	0	0	0	0	2	0
S. glarea	-	0	0	-	-	-	-	1
S. oxyaspis	-	0	0	-	-	-	-	0
S. sittybon	-	0	0	-	-	-	-	0
S. pruinosus	4	0	0	0	0	3	3	0
S. pyretus	4	0	0	2	0	7	3	0
S. armatipes	0	1	1	0	0	0	1	1
S. amplitarsus	4	1	1	0	0	0	3	0
S. viciniger	-	0	0	-	-	-	-	1
Colletes sp.	5	0	0	0	2	0	0	0
Euryglossa sp.	4	0	0	0	0	0	0	?
Hylaeus sp.	5	0	0	0	0	0	0	?

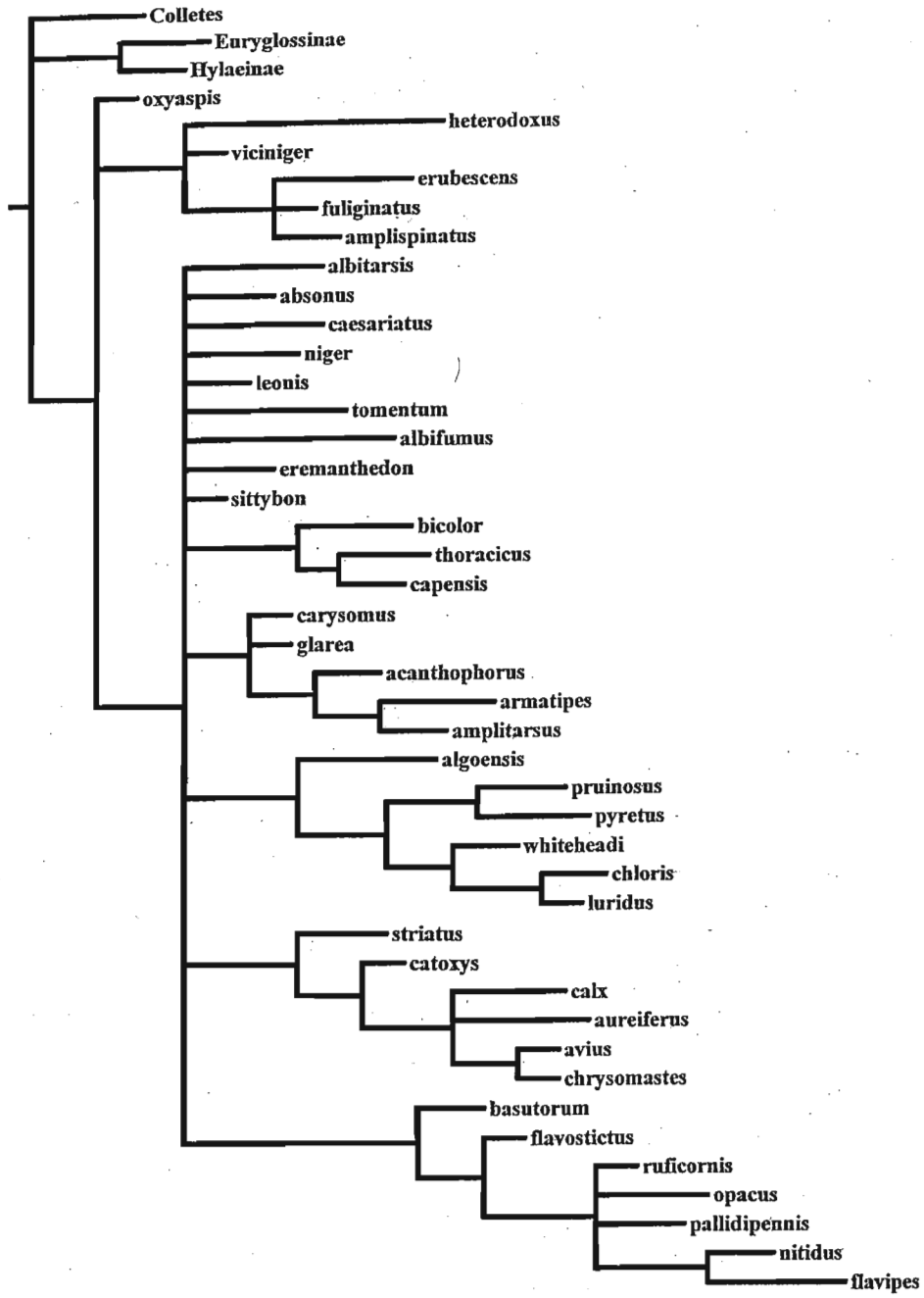


Fig. 174. Strict consensus tree of over 2000 most parsimonious cladograms without character weighting.

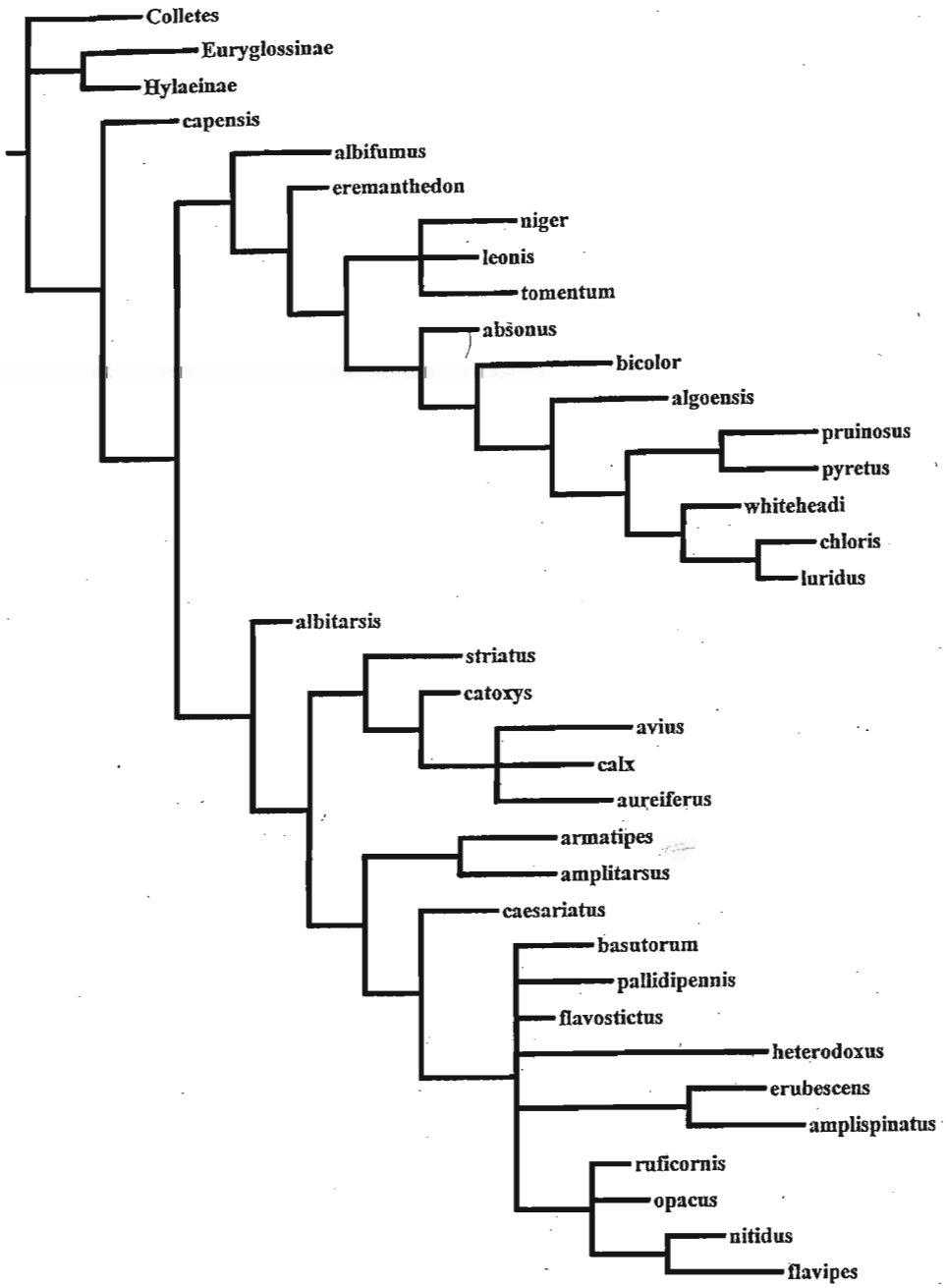


Fig. 175. Strict consensus tree of most parsimonious cladograms without character weighting and using reduced matrix (see text for further details).

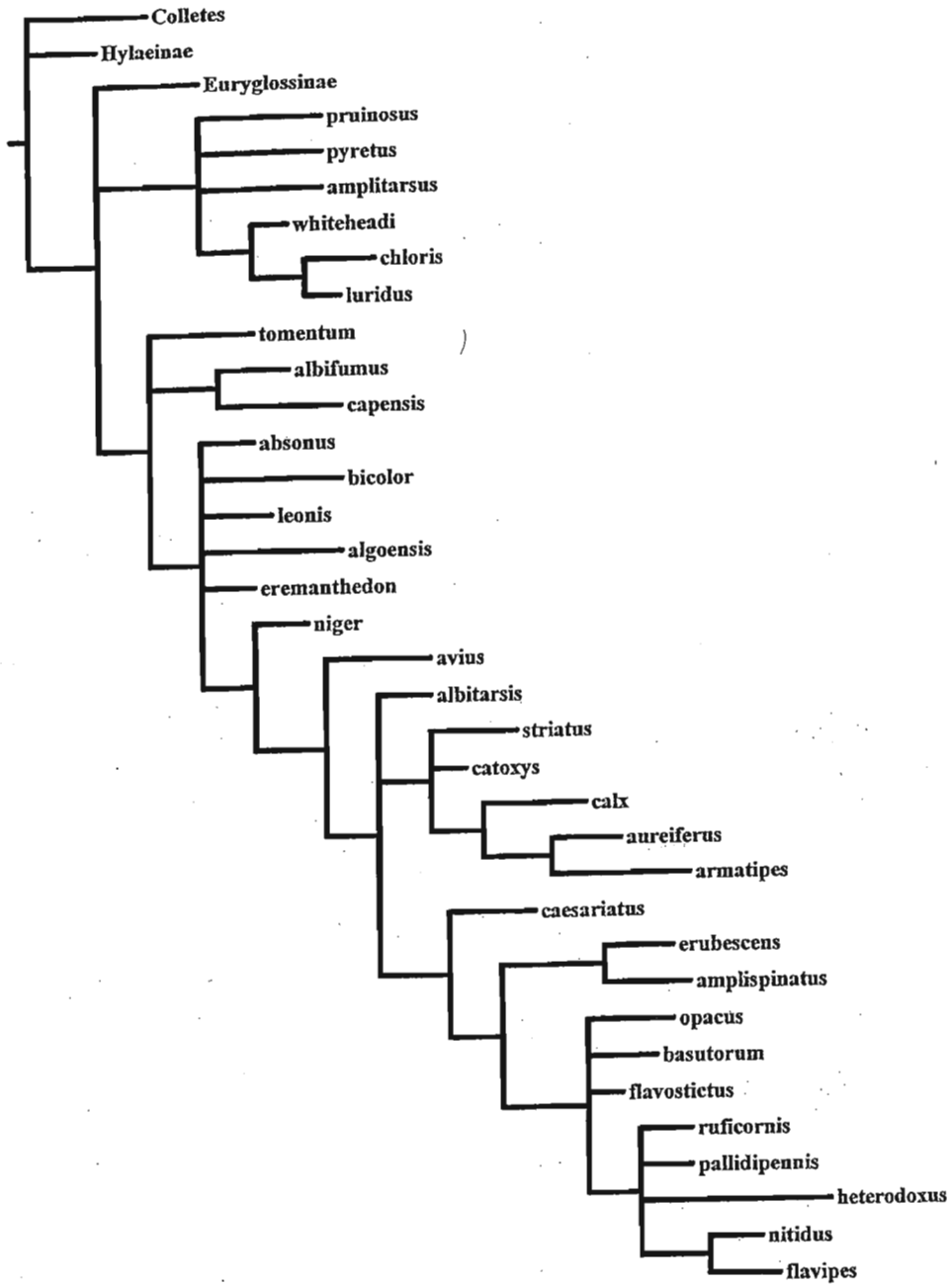


Fig. 176. Strict consensus tree of most parsimonious cladograms using successive-weighting and reduced matrix (see text for further details).